

PALEOECOLOGICAL ANALYSIS OF CHEILOSTOME BRYOZOA FROM VENEZUELA-BRITISH GUIANA SHELF SEDIMENTS¹

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ABSTRACT

The Venezuela-British Guiana continental shelf is a broad, gently seaward-sloping plain with surface sediments characterized by a near-shore silty clay facies which grades seaward into a calcareous sand. In the southern portion of the study area, streaks and prominences of biohermal carbonates occur near the shelf edge. These are considered Pleistocene biohermal relicts of a lower stand of sea.

The cheilostome Bryozoa found in sediment samples collected from 40 stations along the shelf were described and their occurrence was numerically investigated. Q-mode clustering techniques were employed to establish biofacies on the basis of stations bearing similar faunules, and R-mode clustering methods were used to establish "associations" from grouping mutually occurring species. Biofacies and "associations" of Bryozoa and their distribution and composition are discussed and compared to several environmental parameters. Two meaningful "associations" and four biofacies were rendered by the clustering technique.

A strong interrelationship between bryozoan "associations," biofacies, and sediment substrate was noted. The silty clay facies along the inner shelf was virtually devoid of Bryozoa. Between the barren silty clays and the bryozoan-rich calcareous sand of the outer shelf there is a transitional biofacies that is essentially devoid of Bryozoa other than *Nellia tenella*.

A bryozoan "association" characterized by species having lunulitiform zoaria, dominantly *Cupuladria canariensis*, *Discoporella umbellata*, and *Mamillopora cupula*, in association with large quantities of *N. tenella*, was found along the outer shelf. A "sub-association" on the somewhat finer substrate along the outer shelf east of the Orinoco Delta was identified, and is characterized by *Reteporellina marsupiata* and the conical variant of *M. cupula*.

At stations near the shelf edge in the vicinity of the biohermal prominences an "association" of *Canda retiformis*, *Gemelliporina glabra*, *Cel-laria bassleri* and *Setosellina goesi* was recorded. Species diversity attains a maximum in the proximity of the bioherms. The bioherms may provide a source for a redistributed, reworked faunal contribution to the "association" characteristic of the outer shelf.

It was concluded that sedimental substrate is the principal factor influencing the distribution of Bryozoa along the shelf. The effect of the measured environmental hydrographic parameters of temperature and depth on the faunal distribution could not be discerned. If present at all, it is completely masked by the influence of the sediment substrate.

INTRODUCTION

The abundance of cheilostome Bryozoa in many Cenozoic sublittoral

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marine facies, their sedentary existence, minute size, and sensitivity to environmental conditions qualify them as a potentially important tool for paleoecological interpretation. Bryozoa have seldom been used in paleoecological studies, however, because only meager information is available on the relationship between modern Bryozoa and their environmental requirements and tolerances. Nevertheless, the usefulness of employing Bryozoa as a basis for paleoecologic interpretation has recently been demonstrated in studies by Cheetham (1963) and Lagaaij & Gautier (1965).

Distributional patterns of benthonic organisms along continental shelves are due in part to ecological factors and in part to subsequent, postmortem transportation and mixing of the skeletal remains and sediments. The aim of the present study is to examine the environmental and sedimentary conditions that may govern the composition and distribution of thanatocoenose bryozoan associations in Venezuela-British Guiana shelf sediments.

Faunule composition varies quantitatively and qualitatively from station to station; thus the definition of both associations and biofacies has posed a problem common to many paleoecological investigations. An attempt was made in this study to define associations and biofacies numerically on the basis of bryozoan content, by the use of clustering techniques involving R-mode and Q-mode analysis.

Paleoecologic interpretation based on thanatocoenose assemblages depends not only upon principles of ecology, but also upon local sedimentation and geologic history. The study of Bryozoa from sediments along the modern Venezuela-British Guiana shelf has been complemented by data on sediments and the marine environment, and by information on the Recent geologic history of the Venezuela-British Guiana shelf based on sediment studies by Nota (1958) and Koldewijn (1958), and foraminiferal studies by Drooger & Kaaschieter (1958).

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PROCEDURE

Survey Methods.—Data presented in this report are primarily the quantitative occurrences of cheilostome bryozoan species in sediment samples of 40 Phleger cores collected from the USS PREVAIL (AGS-20) for the U. S. Naval Oceanographic Office along the Venezuela-British Guiana shelf during the 14th to 19th of September, 1963. Seventy modified oceano-

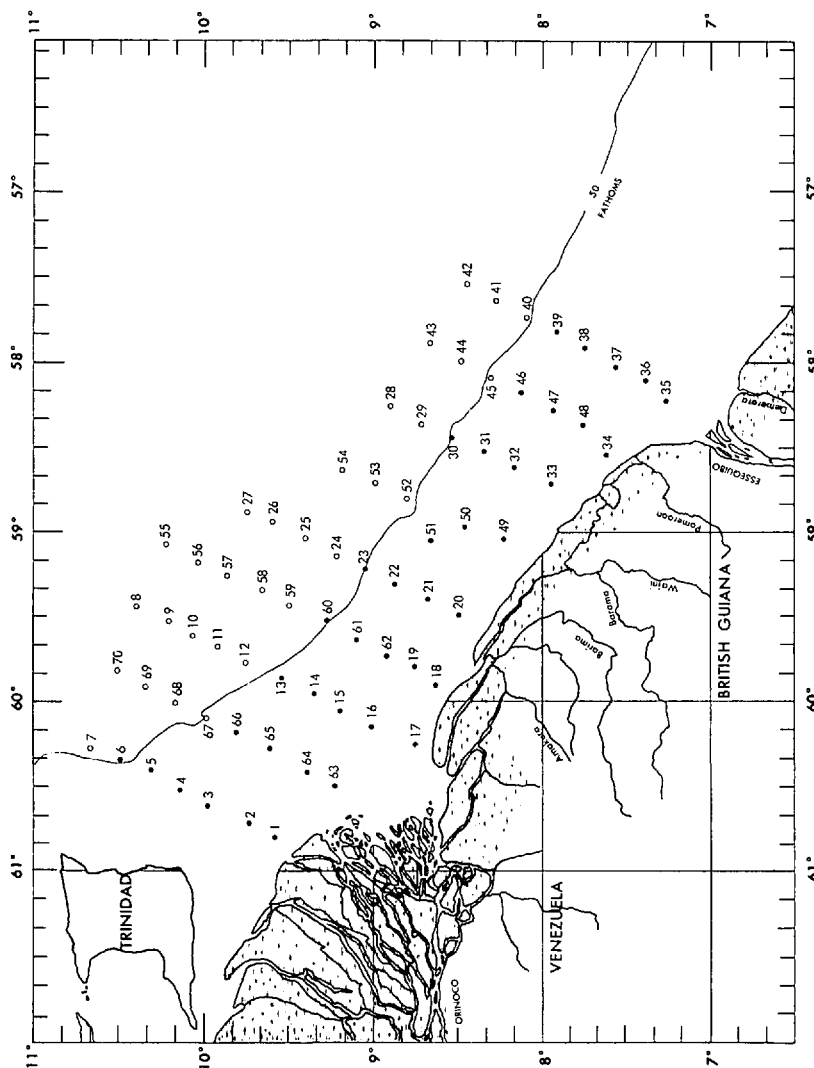


FIGURE 1. Location of consecutive stations along the Venezuela-British Guiana shelf. Solid circles indicate stations at which cores were collected.

graphic stations were occupied along nine traverses normal to the coast between the Orinoco and Essequibo rivers. Cores were collected at the 40 stations located on the continental shelf. Stations along a traverse were occupied at 10 to 12 nautical mile intervals, and the traverses were approximately 20 nautical miles apart. Station locations and the general setting are illustrated in Figure 1.

Oceanographic data collected at the 70 consecutive stations include: 70 determinations of surface temperature and salinity, 46 bathythermograph profiles, and 40 water-temperature measurements at or near the bottom. Positions, dates, numbers of bottom-sediment sample, measurements of surface temperature and salinity, bottom-temperature measurements, and sonic depth are tabulated in Table 2.

Surface temperatures and water samples for salinity analysis were collected at all stations. Temperatures were measured using a standard bucket thermometer. Water samples were sealed in citrate bottles. Salinities were determined by using an inductively coupled salinometer.

Sediment samples were obtained with a Phleger corer, and bottom-water-temperature measurements were made at core stations. The cores were capped, sealed with microcrystalline wax, and shipped to the U. S. Naval Oceanographic Office for analysis of sediment size and composition.

Several short fathograms were run, to illustrate some of the bathymetric detail along the Guiana shelf. However, because of the lack of precision navigational aids during the cruise, no bathymetric survey was conducted. Navigation was accomplished by celestial and radar fixes taken at the stations occupied.

Laboratory Methods.—The cores were examined, and the visually recognizable changes in sediment were recorded. Analyses of sediment size and carbonate content were performed on 155 samples cut from the cores, and small portions of the samples were saved for reference. The carbonate concentration was determined by the insoluble residue method described by Twenhofel & Tyler (1941).

Sediment samples were analyzed for grain-size distribution. The sediment was wet-sieved with dilute calcium hexametaphosphate (Calgon) solution through a 0.062-mm screen. The coarse fraction retained on the screen was dry-sieved at one-phi intervals, and the fine fraction was pipetted at two-phi intervals by standard procedures outlined by Krumbein & Pettijohn (1938).

The carbonate content and textural measures are discussed more completely in the sections dealing with bottom sediments and factors controlling distribution of Bryozoa. The convention followed for the nomenclature of sediment texture is based on Shepard's (1954) sediment triangle.

Fragments of the cheilostome bryozoan colonies were picked from the

fractions of the sediment samples coarser than 0.25 mm, and counted. The number of zoarial fragments in the fractions finer than 0.25 mm was found to be insignificant, usually less than one per cent of the total quantity present; generally they belonged to one species, *Nellia tenella*. The slender, prismatic internodes of this species pass through the 0.25-mm mesh much more easily than fragments of other species do.

The bryozoan fragments picked from each sample were identified as to species, and the number of specimens of each species was recorded. Taxonomic and nomenclatural notes on the species identified are presented in the systematic section of this report. Bryozoan specimens were photographed by means of a Polaroid MP 3 camera in combination with a Bausch & Lomb (BG-525) binocular microscope. The film used was Polaroid film type 107 (3000 ASA equivalent). Photographs were not retouched, but, in order to accentuate minute details and to reduce hyaline glare, specimens were lightly stained with red vegetable dye and then lightly whitened with ammonium chloride.

ENVIRONMENTAL AND PHYSICAL SETTING

The study area extends along the continental shelf from the vicinity of the Orinoco Delta to the mouth of the Essequibo River (Fig. 1). Shoreward, southwest of the study area, lies the low coastal province of Venezuela-British Guiana. Between the Orinoco and Essequibo rivers, the coast is wooded and swampy, and has low relief (U. S. Naval Oceanographic Office, 1952).

Coastal Geomorphology and Stratigraphy.—The coastal province is a seaward-sloping wedge of Cenozoic sediments. Although the exact configuration of the sedimentary wedge is poorly defined, it is known that the sediments thicken to seaward, and thin to the southwest where they rest upon the igneous-metamorphic Paleozoic basement of the stable Guiana Shield.

The stratigraphy of the coastal sediments has been described in detail by Vann (1959), Grantham & Noel-Paton (1937), and Bleackley (1956). Bleackley described three stratigraphic units that comprise the coastal sedimentary wedge: (1) the White Sand Series, (2) the Coropina Formation, and (3) the Demerara Clay. The White Sand Series and Coropina Formation are Plio-Pleistocene sequences of sands and clays 100-300 feet thick, and are physiographically expressed as elevated, dissected remnants of depositional terraces. The Demerara Clay, a soft blue clay, 100 feet thick in some places, is considered to be entirely of postglacial age. It overlies the Coropina Formation. The low, wooded marshlands of the coastal province generally coincide with the distribution of the Demerara Clay, which is also thought to extend to seaward a considerable distance (Worts, 1963).

Climate.—The meteorological data presented below are summarized from data published in "Sailing Directions for South America" (U. S. Naval Oceanographic Office, 1952: 301).

The tropical climate of the Venezuela–British Guiana coastal province is dominated by pronounced, double, wet-and-dry seasons. The primary rainfall maximum is in June, and a secondary, relatively stormy maximum is reached in December. The primary and secondary dry seasons occur in October and February, respectively. Even during the dry seasons, however, rain falls nearly one out of three days. The annual average rainfall is between 198 and 228 cm per year. This warm, wet, tropical climate influences several marine environmental factors which are considered in this study.

Temperatures along coastal British Guiana are nearly constant. The monthly mean temperatures rarely depart from the annual average of 26.7°C by more than a degree.

The coast is swept by moderate 5- to 8-knot northeast tradewinds most of the year. The velocity of winter surface winds recorded at Georgetown seldom exceeds 8 knots, dropping to near 5 knots in the summer. The average annual wind velocity is about 6 knots.

Water Temperature.—Surface temperatures, measured at all stations, varied only slightly throughout the surveyed area. Temperatures in nearshore waters were slightly warmer than those recorded farther offshore (29–30°C vs. 28–29°C). The cooler temperatures of offshore waters are due to advective mixing with deeper, cooler waters. The seasonal variation in surface waters is slight, usually less than one degree, reflecting the constancy of the tropical climate (U. S. Oceanographic Office, 1963).

A stable thermal structure with little seasonal variation is indicated by the warm surface waters and the lack of seasonal variability of the surface-water temperatures. A composite envelope of temperature-depth profiles was constructed from bathythermograms which displayed considerable congruency in this area. In general, bottom temperatures measured at core stations fell within the composite envelope (Fig. 2, inset) and varied only slightly from surface temperatures (26.5–29.5°C) down to depths of 10 or 12 fathoms due to surface mixing. Beneath the mixed layer, temperatures decreased gradually. The temperature was near 24°C along the shelf edge, between 40 and 50 fathoms.

Salinity.—Surface salinities were measured at all 70 stations during the survey period in mid-September, 1963, shortly after the normal August peak discharge of the Orinoco River. The extensive fresh-water wedge of plume of the Orinoco was clearly evidenced by surface salinities of less than 32‰ at stations 40 miles to seaward from the mouths of the Orinoco. Normal marine surface salinities between 35 and 36‰ were measured

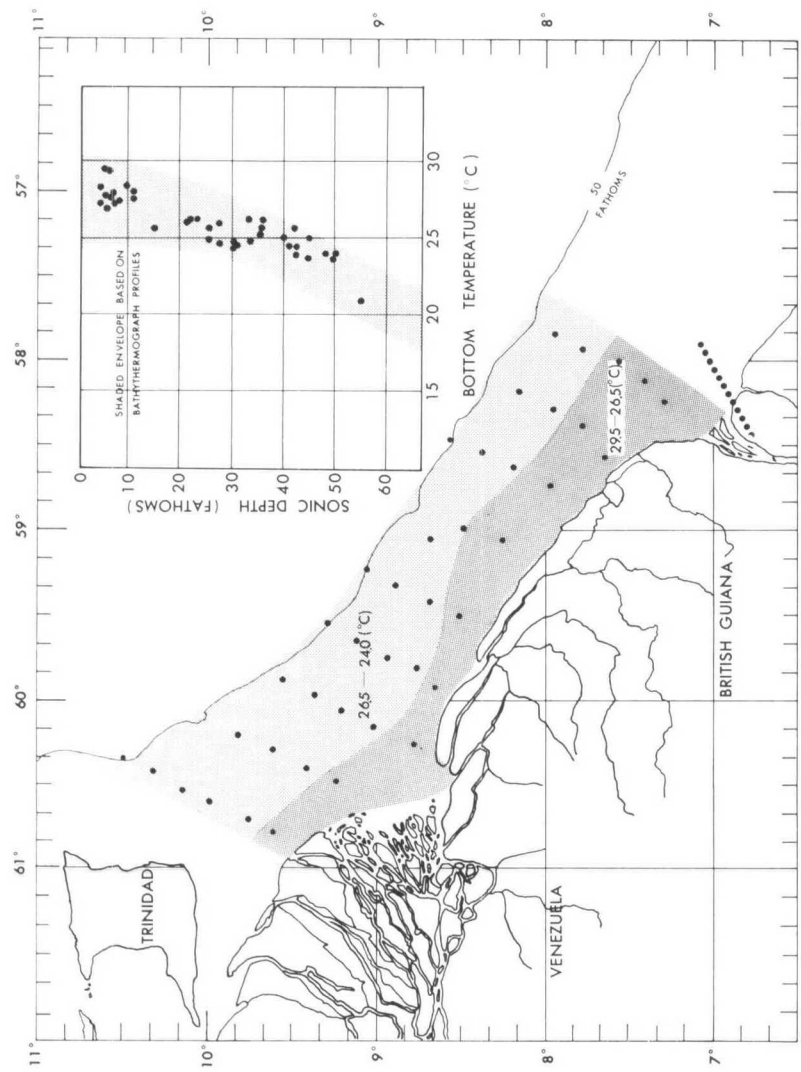


FIGURE 2. Distribution of bottom temperature, and composite profile of temperature with depth.

throughout most of the remainder of the survey area seaward and south of the Orinoco fresh-water plume. The only exception was a slightly reduced salinity of 32‰ at core station 23, due to the effluence of the Essequibo River.

Neither the discharge of the Orinoco nor that of the Essequibo responds to the double wet-and-dry seasons of the coastal climate. The coastal rainfall, however, is of considerable importance in controlling the discharge of the several small rivers which drain the coastal plain between the Orinoco and Essequibo rivers (Worts, 1963). As the survey was conducted during the height of the "long," or "primary," dry season, the extent of the influence of seasonal coastal drainage on the nearshore surface salinities is unknown.

The salinity near the bottom is a far more important ecological consideration in this study than is the surface salinity. It is a factor capable of limiting the distribution of sedentary stenohaline marine organisms such as most cheilostome Bryozoa. Unfortunately, no bottom salinity measurements were made during this survey, and thus it is not possible to determine quantitatively the degree of influence exerted on the bryozoan associations by the bottom salinities.

Judging from the surface salinity distribution, it would seem that the bottom throughout the entire study area should be accessible to numerous species of cheilostome Bryozoa with regard to salinity, except for stations near the Orinoco Delta. The exact extent to which the widespread fresh-water plume affects the bottom salinities along the delta platform is not known.

BATHYMETRY

The gentle slope of the broad, relatively smooth Venezuela-British Guiana continental shelf is abruptly interrupted by the shelf edge at depths between 40 and 50 fathoms. In the southern portion of the study area, the shelf is about 60 miles wide. From the shelf edge, the slope descends rapidly to depths greater than 1,000 fathoms in less than 30 miles. In the northern portion of the area the shelf is broad, and the gradient of the continental slope is gentle. The comparatively broad northern shelf and slope may be structurally related to the elevated basement complex of the Barbados Plateau (Koldewijn, 1958). The general bathymetry and the tracks of four bathymetric profiles are indicated in Figure 3.

The Orinoco Delta has probably not yet advanced seaward over the continental shelf. The outer limits of the Orinoco Delta platform and delta front extend seaward to depths of approximately 30 fathoms (van Andel *et al.*, 1954). Bathymetric profile d-d' (Fig. 6) parallels the coast near the Orinoco Delta and shows a section of the prograding delta front that is building out over the inner shelf floor. The inset enlargement of

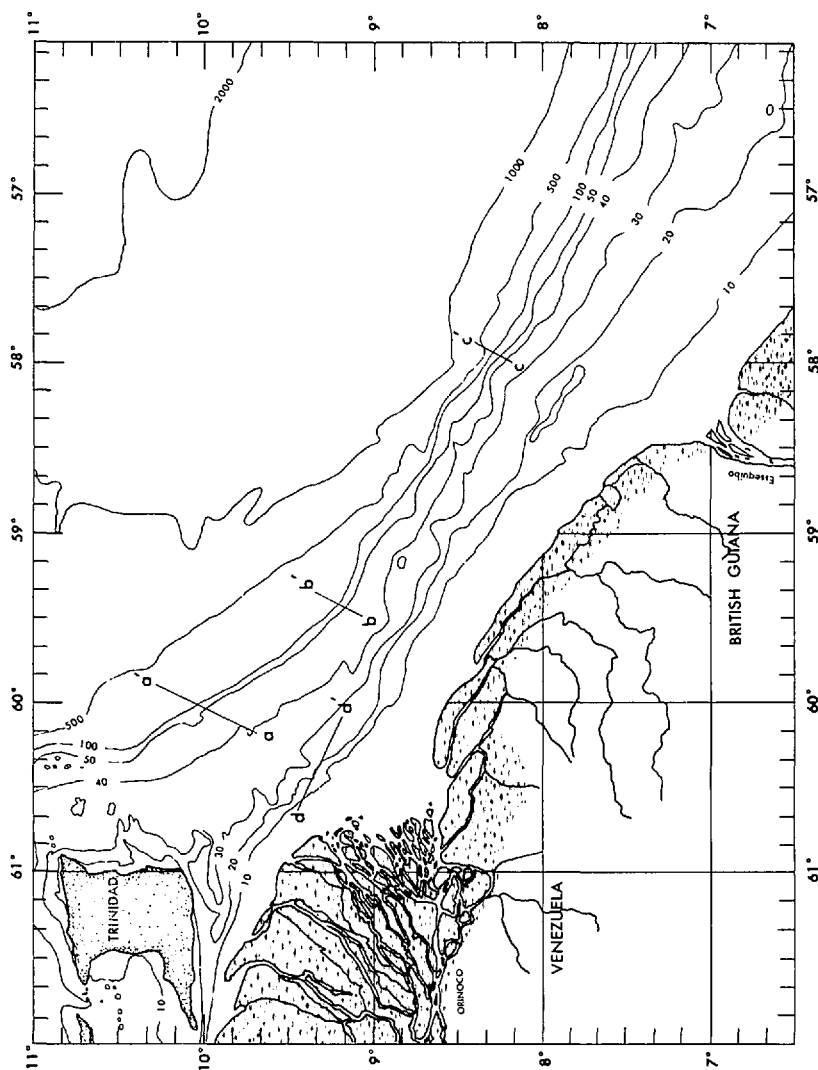


FIGURE 3. General bathymetry and location of bathymetric profiles based on U. S. Naval Oceanographic Office charts BC 602 and BC 603. Depth in fathoms.

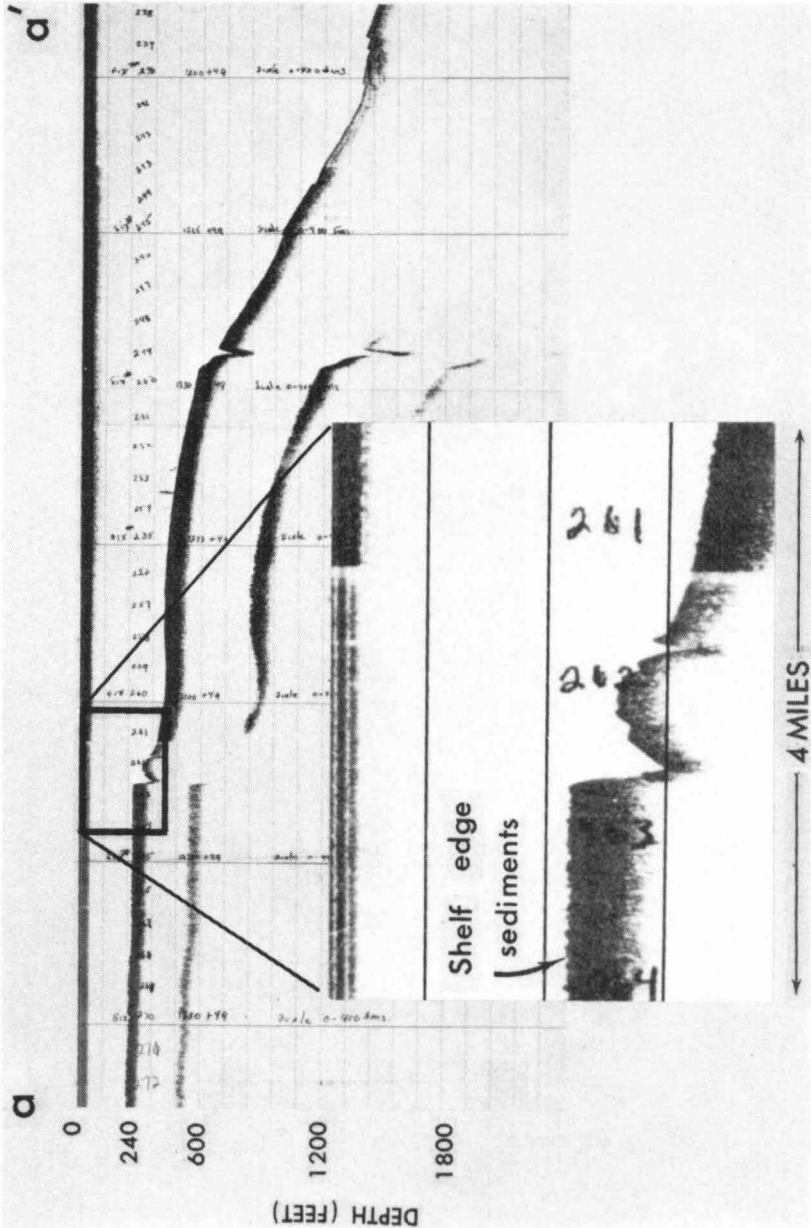


FIGURE 4. Precision depth recorder profile a-a'. Outer shelf and shelf edge east of the Orinoco Delta.

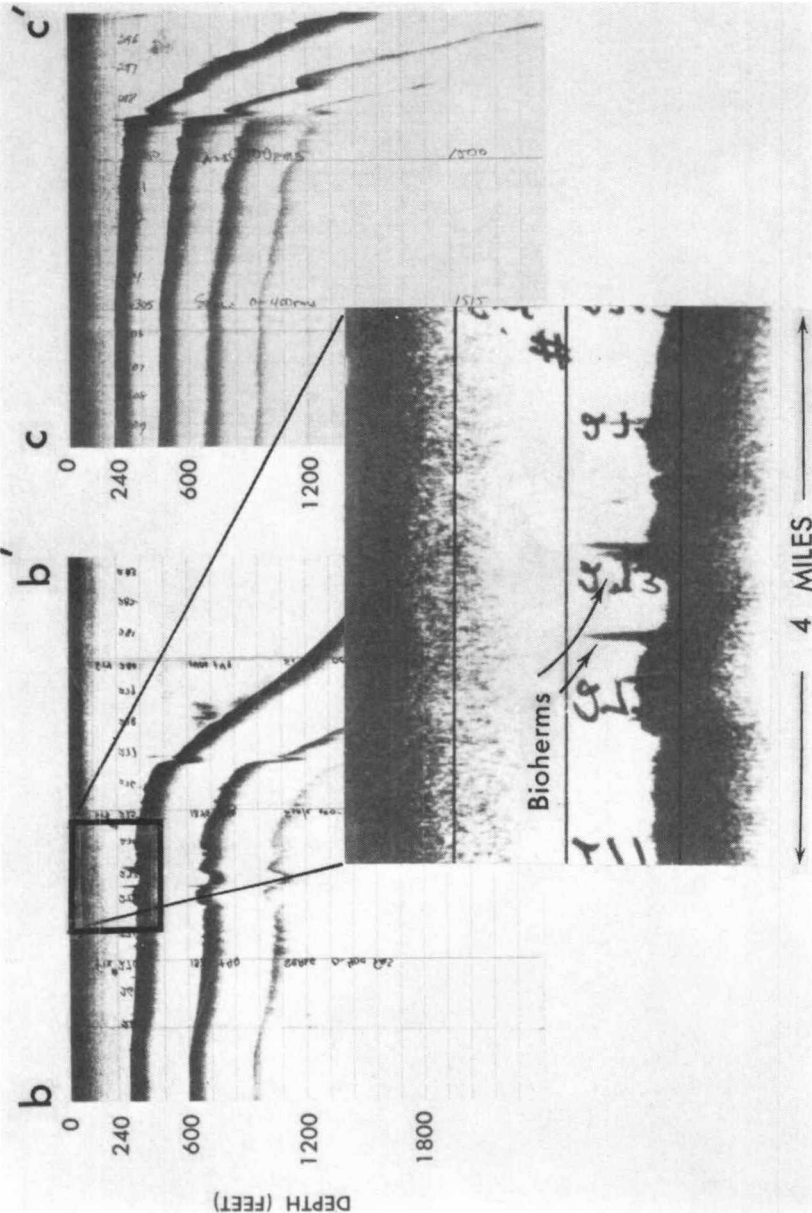


FIGURE 5. Precision depth recorder profile b-b' and c-c'. Shelf-edge biohermal features are well developed in profile b-b'.

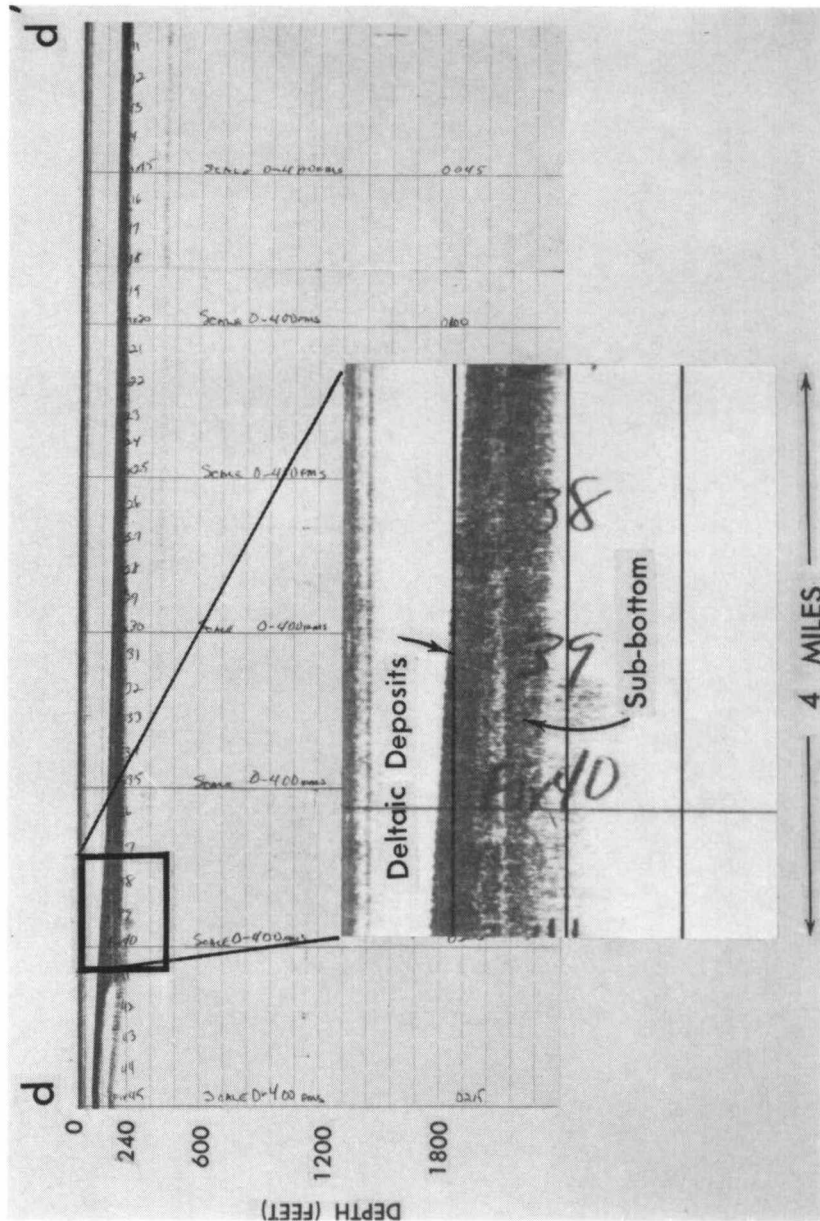


FIGURE 6. Precision depth recorder profile d-d'. Soft deltaic sediments wedge out over an older sub-bottom.

a portion of this profile shows an older subbottom reflective layer beneath the surface of the modern delta front.

The Essequibo delta front only extends to approximately the 10-fathom contour, where it grades onto a rather broad platform at a depth between 10 and 20 fathoms. A submarine ridge parallels the present shoreline along the seaward edge of the platform between 10 and 12 fathoms (Fig. 3). Nota (1958) has demonstrated that this feature may be a drowned sand-ridge system associated with a 12-fathom, postglacial stand of sea level. An analogous, modern, beach and sand-ridge complex has formed along the shoreline northwest of the Essequibo Estuary.

The outer shelf is characterized by a surface that slopes gently seaward to the shelf edge. On the basis of closely spaced, minor (1-2 fathom) irregularities on the fathogram record, the outer shelf is thought to have a rough surface. An enlargement of a portion of section a-a', near the 40-fathom depth, illustrates this roughness (Fig. 4). Nota (1958) interpreted the minor irregularities of the outer shelf as drowned shoreline features, such as sand ridges and dunes, associated with a 40-fathom stand of sea level, which have been modified by the transgressing sea.

Features described as reef-like prominences by Nota (1958) were frequently recorded near the shelf edge. These prominences rise as much as 5 to 10 fathoms above the general surface of the sea floor, and seem to be more prevalent along the southern portion of the study area. The prominences can be seen clearly on the enlargement of section b-b' in Figure 5.

SHELF SEDIMENTS

In spite of the remoteness of the Venezuela-British Guiana shelf, the sediments and recent depositional history of this area are well known. These sediments were studied in considerable detail by Nota (1958). Koldewijn (1958) studied the sediments of the Paria-Trinidad shelf north of, and contiguous with, Nota's area. The extent of the area presently under investigation is virtually coincident with that of Nota's study; only core stations 4, 5, and 6 fall in the area studied by Koldewijn. The distribution of the shelf Foraminifera was treated exhaustively by Drooger & Kaaschieter (1958). Their study was based on the washed residue from samples studied by Nota and by Koldewijn.

On the basis of median grain size and carbonate content, the sediments along the shelf were divided into several lithofacies that agree closely with the sediment distribution described by Nota (1958) and Koldewijn (1958). When several sediment facies were represented in a single core, it was possible to suggest a sequence of sedimentary events. The cores available for this study, however, were too short and too widely spaced to be employed for purposes of stratigraphic correlation between cores.

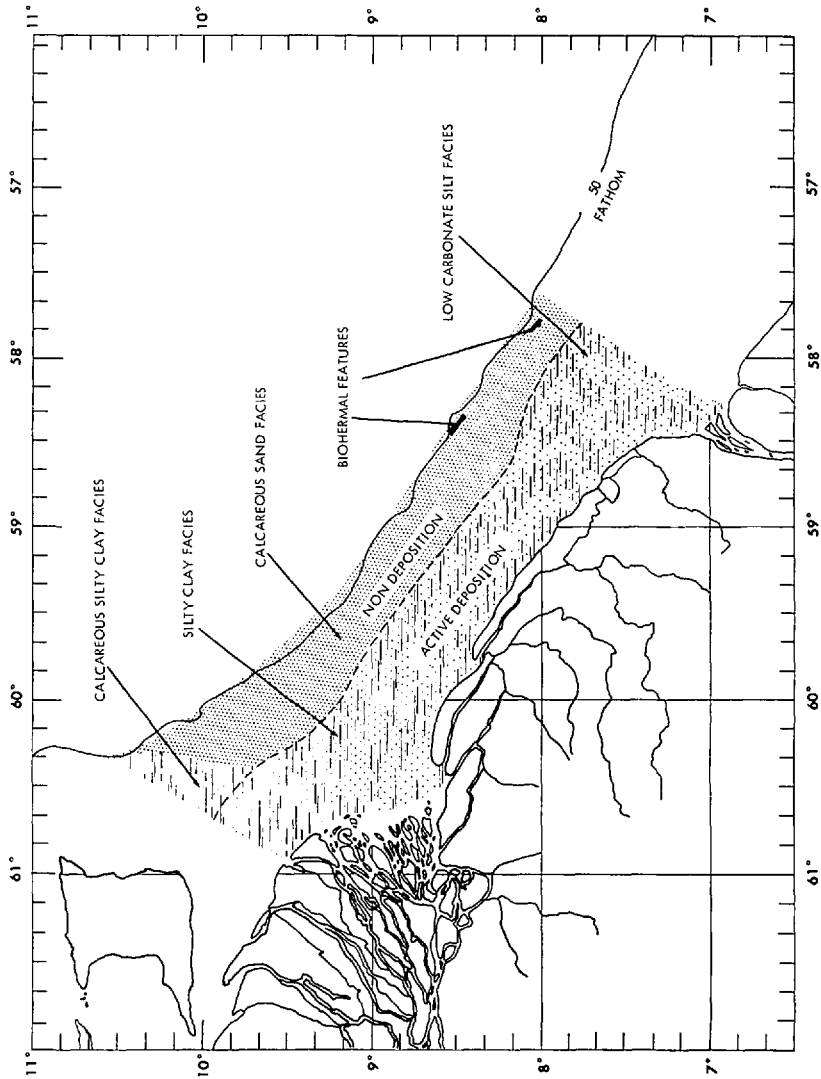


FIGURE 7. Distribution of sedimentary facies.

The general distribution of these surficial sedimentary facies is indicated in Figure 7.

SEDIMENT FACIES OF THE OUTER SHELF

Calcareous Sand Facies.—Surficial sediments along the outer shelf are characterized by an extensive calcareous sand facies which has a relatively high carbonate content (20-40 per cent) and a median grain diameter of less than 4 phi units. The high carbonate content is due to large quantities of invertebrate skeletal detritus which consists chiefly of Foraminifera, with somewhat fewer fragments of molluscs and bryozoans. *Amphistegina lessonii*, because of its large size and abundance, is the most conspicuous of the Foraminifera. The skeletal fragments are generally worn and iron-stained.

The carbonate content in cores 18 and 27 was found to be 90 and 43 per cent, respectively. These sediments are interpreted as patches of calcarenite derived from nearby biohermal prominences of the shelf edge. In this study, these biohermal accumulations were clearly recorded in bathymetric profiles taken near the shelf edge. They were also reported by Nota and Koldewijn. On the basis of radiocarbon measurements on consolidated calcareous material dredged from the biohermal features near the shelf edge at depths of approximately 40 fathoms, Nota found the age of these sediments was between $11,560 \pm 240$ and $17,550 \pm 110$ years. Ages in excess of 11,000 years for the drowned biohermal features at 40 fathoms agree closely with sea-level stands determined by other investigators (Shepard, 1956, 1960; Curray, 1960; Fisk & McFarlan, 1955; McFarlan, 1961).

Nota (1958) postulated that the calcareous sands along the outer shelf and the shelf-edge biohermal prominences were deposited essentially simultaneously during the lower stand of sea (40 fathoms) in the Pleistocene (approximately 11,000 years before present). Fluvial sands deposited at the Pleistocene shoreline were reworked by longshore littoral processes and redistributed as beach-ridges or "cheniers." The beach-ridge sands and biohermal detritus from offshore reefs were subsequently mixed and spread landward by the transgressing sea. The combined effect of shelf-edge, wave-induced turbulence and the flow of the North Equatorial Current preclude significant deposition of fine suspended sediments during the postglacial period. Although the outer shelf is now submerged to depths of approximately 40 fathoms, large storm waves may produce some winnowing, reworking, and landward spreading of the sands along the outer shelf. Evidence of the shoreward spreading of the calcareous sand facies was found in cores 9, 40, 7, and 34, where 10 to 25 cm of calcareous sand overlies a distinctly different clay or silt facies.

The concept of continuous reworking and mixing of the outer shelf

sands advanced by Nota (1958) is supported by two lines of evidence. First, the rather homogeneous composition of the sands, and the presence throughout the core profiles of both worn and stained specimens of the foraminiferan *Amphistegina lessonii*, along with specimens which have a fresh and unabraded appearance. Second, radiocarbon dates of between $5,600 \pm 150$ and $5,630 \pm 160$ years before present were obtained for specimens of *Amphistegina lessonii* picked from sediment samples from core depths of 10 and 180 cm respectively. These carbon-14 dates were interpreted by Nota to be obtained from a mixture of Recent and sub-Recent specimens. If this second line of evidence is correct, it requires that the unworn specimens of *A. lessonii* are elements of modern, still-living fauna.

Calcareous Silty Clay Facies.—A silty clay facies was found at core stations 4, 5, and 6. These sediments differ from the widespread, coastwise, silty clay facies of the inner shelf. Although their median grain size is similar ($> 8 \phi$), the carbonate silty clay facies is distinguished by a greater content of sand-sized constituents, and it is somewhat more calcareous (15-20 per cent).

The calcareous silty clay facies is a product of an environment of slow deposition along the current-swept outer shelf (van Andel & Postma, 1954). Its distinct carbonate aspect may be due, in part, to its proximity to the carbonate accumulation of the eastern Trinidad shelf reported by Koldewijn (1958).

SEDIMENT FACIES ALONG THE INNER SHELF

Silty Clay Facies.—The coastal and inner shelf are environments of high rates of deposition. Large quantities of fine sediment are carried by the northwestward, longshore current (Vann, 1959). The bottom sediments along the inner shelf are dark, homogeneous, silty clays, typically characterized by low carbonate content (10 per cent) and a median grain diameter of greater than eight phi units. These sediments are virtually devoid of carbonate skeletal detritus. Seaward of this barren zone, the abundance and diversity of carbonate skeletons gradually increase.

The extensive low-carbonate, silty clay facies paralleling the coast thins seaward onto, or becomes mixed with, the calcareous sand facies which characterizes the outer shelf. At core stations 38, 39, 9, and 35, the surficial silty clay, or silty clay and calcareous sand mixture, grades rapidly into an underlying calcareous sand facies. The mixture of silty clay and calcareous sand is characterized by a bimodal distribution of grain size, with one mode in the clay range, and the other in the sand range. Its median grain diameter ranges from approximately 4 to 8 phi units and its carbonate content varies between 10 and 20 per cent.

Sediments essentially identical to the coastwise silty clay facies of the

inner shelf were found beneath the calcareous sands in the lower portions of several cores (40, 7, 34, and 28) collected at stations near the shelf edge. The sediment in the lower portions of cores 7 and 34 is a low-carbonate silt, or a fine clayey sand, similar to the silty fluvial sediments presently being deposited near the mouths of the Essequibo and Orinoco rivers (van Andel & Postma, 1954; Nota, 1958). The low-carbonate, clayey silt facies are described in the following section.

The discovery of what appear to be nearshore or inner-shelf sediments beneath the calcareous sands along the outer shelf near the shelf edge suggests that these sediments were deposited during the Pleistocene 40-fathom stand of sea level. Their deposition in shallow water was probably contemporaneous with the deposition of the beach-ridge sands or "cheniers" along the Pleistocene (40-fathom) shoreline, and possibly with the offshore calcareous biohermal accumulation.

Low-carbonate Silt Facies.—The drowned beach-ridge system lying seaward of the Essequibo River at 10 to 12 fathoms is surfaced with sediments consisting of a low-carbonate silt or a fine clayey sand. These sediments characteristically contain less than 15 per cent carbonate, and have a median grain diameter ranging from approximately 3 to 7 phi units.

The low-carbonate silts and fine clayey sands that occur at core stations 30, 29, 25, and 24 appear to be fluviomarine sediments derived from the drowned beach-ridge system which forms the seaward boundary of the facies distribution. This drowned ridge system has been previously discussed in the section on bathymetry.

Nota (1958) reported these drowned beach ridges, and determined that they were chenier-like ridges related to a 12-fathom stand of sea level. On the basis of carbon-14 dates by other authors (Bennema, 1954; Schmitz, 1954; Shepard & Suess, 1956), Nota estimated that the 12-fathom stand of sea took place approximately 8,000 years B.P. Radiocarbon dates on drowned shoreline features subsequent to Nota's report tend to strengthen his estimate of 8,000 years B.P. for a 12-fathom, still stand (Godwin *et al.*, 1958; Fairbridge, 1958; Curray, 1960).

SUMMARY OF DEPOSITIONAL HISTORY

The present-day continental shelf was exposed to subaerial conditions as a low coastal plain during the Pleistocene (approximately 11,000 yrs B.P.) stand of sea level (40 fathoms). The river courses extended across the coastal plain, and fluviomarine deposition took place virtually at the edge of the continental shelf. Intense wave, and littoral transport occurred along the 40-fathom shoreline that was exposed to long-period oceanic waves, whose intensity was not reduced by friction during progress across a broad continental shelf. An extensive plain of silty clay and clayey marsh flats, as well as elongate, chenier, beach-ridge sands are believed

TABLE 1
DATA ON OCCURRENCE OF BRYOZOA¹

	No. of samples in which species was found	Maximum No. specimens in any sample	Total No. of specimens
Principal Species			
<i>Nellia tenella</i>	65	587	4,621
<i>Cupuladria canariensis</i> (sensu lato)	51	79	631
<i>Discoporella umbellata</i>	39	18	155
<i>Mamillopora cupula</i> (Encrusting)	33	20	112
<i>Mamillopora cupula</i> (Conical)	31	13	106
<i>Mamillopora cupula</i> (Discoidal)	26	8	92
<i>Scrupocellaria regularis</i>	29	18	136
<i>Setosellina goesi</i>	26	26	122
<i>Celleporaria</i> sp.	22	25	196
<i>Floridina antiqua</i>	20	8	48
<i>Cellaria bassleri</i>	18	6	46
<i>Reteporellina marsupiata</i>	18	43	142
<i>Gemelliporina glabra</i>	17	14	43
<i>Canda retiformis</i>	15	29	134
<i>Steganoporella magnilabris</i>	13	5	20
<i>Metrarabdotos tenue</i>	12	5	30
<i>Biflustra savartii</i>	11	12	26
<i>Gemelliporella prevailae</i> , n. sp.	10	8	27
Minor Species			
" <i>Stylopoma spongites</i> "	10	4	14
<i>Tremogasterina lanceolata</i>	9	3	14
<i>Hippoporidra janthina</i>	6	2	8
<i>Rimulostoma?</i> <i>signatum</i>	5	7	13
<i>Scrupocellaria maderensis</i>	4	2	5
<i>Labioporella granulosa</i>	4	1	4
<i>Antropora typica</i>	4	1	4
<i>Vittaticella uberrima</i>	3	1	3
<i>Crassimarginatella leucocypha</i>	3	1	3
<i>Escharina pesanseris</i>	3	1	3
<i>Parasmittina spatulata</i>	2	15	16
<i>Parellisina curvirostris</i>	2	1	2
<i>Chaperia condylata</i>	2	3	4
<i>Cleidochasma porcellanum</i>	2	2	3
<i>Cribrilaria</i> sp., aff. <i>C. radiata</i>	2	2	5
<i>Lagenicella marginata</i>	2	1	2
<i>Hippopetraliella marginata</i>	2	1	2
<i>Anarthropora coccinella</i>	2	1	2
<i>Tubucellaria</i> sp.	2	1	2
<i>Hippaliosina rostrigera</i>	1	1	1
<i>Microporella ciliata</i> (sensu lato)	1	3	3
<i>Tremoschizodina lata</i>	1	2	2
<i>Smittipora levinsoni</i>	1	1	1
<i>Retevirgula tubulata</i>	1	1	1

¹ Complete sedimentological and oceanographic data, along with counts of bryozoan specimens at each station, are on file at the National Oceanographic Data Center, Washington, D. C. (NODC Geology Acquisition No. 082366-1).

to have developed along the coastline. Simultaneously, in somewhat deeper waters a few miles offshore, biohermal patches accumulated.

A Holocene transgression of the sea, associated with a rapid, eustatic rise in sea level, took place approximately 11,000 years ago. It drowned the shelf-edge bioherms, and spread shoreward a veneer of littoral and chenier, beach-ridge sands mixed with biohermal debris.

The drowned beach-ridge system to seaward and to the northeast of the mouth of the Essequibo provides evidence of a 12-fathom stand of sea level. These drowned beach ridges are believed to have formed about 8,000 years before present, when the rate of the rise in sea level abruptly decreased. Subsequent transgression of the sea to the modern shoreline position has been comparatively gradual.

Modern sedimentation is taking place along the coastal and inner shelf. The outer shelf is an area of nondeposition. The long-period ocean swell and the strong, northwest, North Equatorial Current along the outer shelf prohibit the deposition of fine-grained sediment.

ANALYSIS OF BRYOZOAN DATA

A total of 40 species of cheilostome Bryozoa belonging to 39 genera were identified, including one new species, *Gemelliporella prevailae*. Every bryozoan fragment in each sample was identified and counted. The number of specimens of each species was recorded for 155 sediment samples weighing 4 to 51 grams, and averaging 12 grams; frequencies were recalculated as number of specimens per 10 grams of original sample, in order to make relative frequencies of species in different samples comparable.

Although the figures for the different samples are numerically comparable after this "normalization," some bias still remains, due to the improved possibility of finding quantitatively minor species in the larger samples. To reduce this bias, species which occurred in fewer than six samples and in quantities of less than eight specimens in the most abundant sample were considered minor constituents and were not included in the numerical analysis of the bryozoan faunules. The 18 most abundant bryozoan species and morphological variants indicated in Table 1 have been included as variables in the numerical analysis.

The numerical treatment used in this study is the cluster analysis of correlation coefficients, a method advanced by Sokal & Sneath (1963) for numerical taxonomy. The method can, however, be applied with equal facility to the grouping of species (variables), in terms of their occurrence in the surface sediments at the 40 core-station locations (cases), into clusters of associated species or "associations." This form of procedure is known as R-mode. The same basic information may also be analyzed in the Q-mode. In Q-mode analysis, attention is focused on the relation-

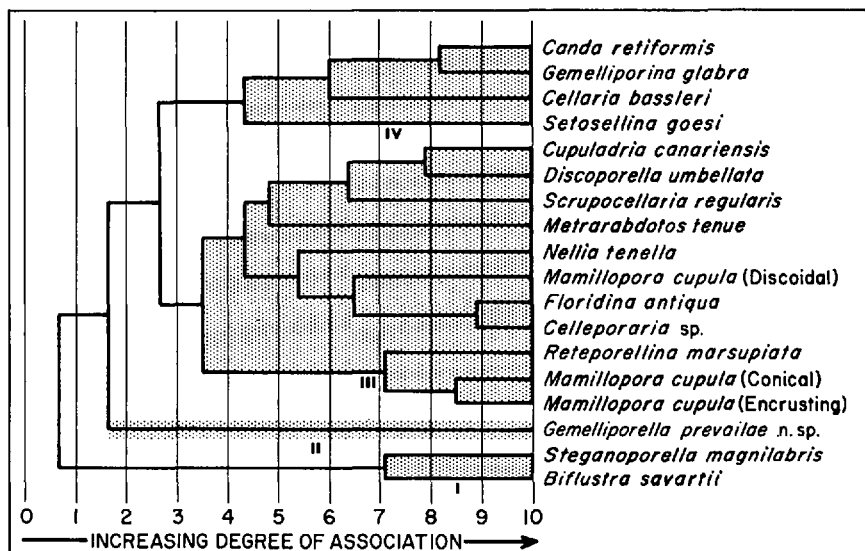


FIGURE 8. Bryozoa "association" clusters (R-mode).

ships between the core stations (cases), explained in terms of the species (variables) found at each station. The Q-mode analysis groups core stations into clusters which have a similar faunal aspect or biofacies.

Analyses were based on counts of bryozoan fragments from the surficial sediment facies only. Fragment counts from the sediment subsamples were combined. The combined counts were then "normalized" by dividing by the total weight of the sediment subsamples, and multiplying the quotient by ten.

R-mode Cluster Analysis for Bryozoan "Associations."—The R-mode analysis involved first the computation of the correlation coefficients among the frequencies of the principal species. Because the variance of the correlation coefficient depends on the value of the coefficient, a transformation of all correlation coefficients from r to Fisher's z was made. The variance of this transformed (z) coefficient is independent of the value of the coefficient (Snedecor, 1946; McNemar, 1959; Sokal & Sneath, 1963). The transformed coefficients were arranged in an initial (18×18) variable matrix. Variables having the highest mutual correlation were then combined by averaging the coefficients in their rows and columns. The process of combining the rows and columns of variables having highest mutual correlation and the recalculation of coefficients for new theoretical or composite variables were repeated until all species had been clustered. Because the unweighted group method (Sokal & Sneath, 1963:

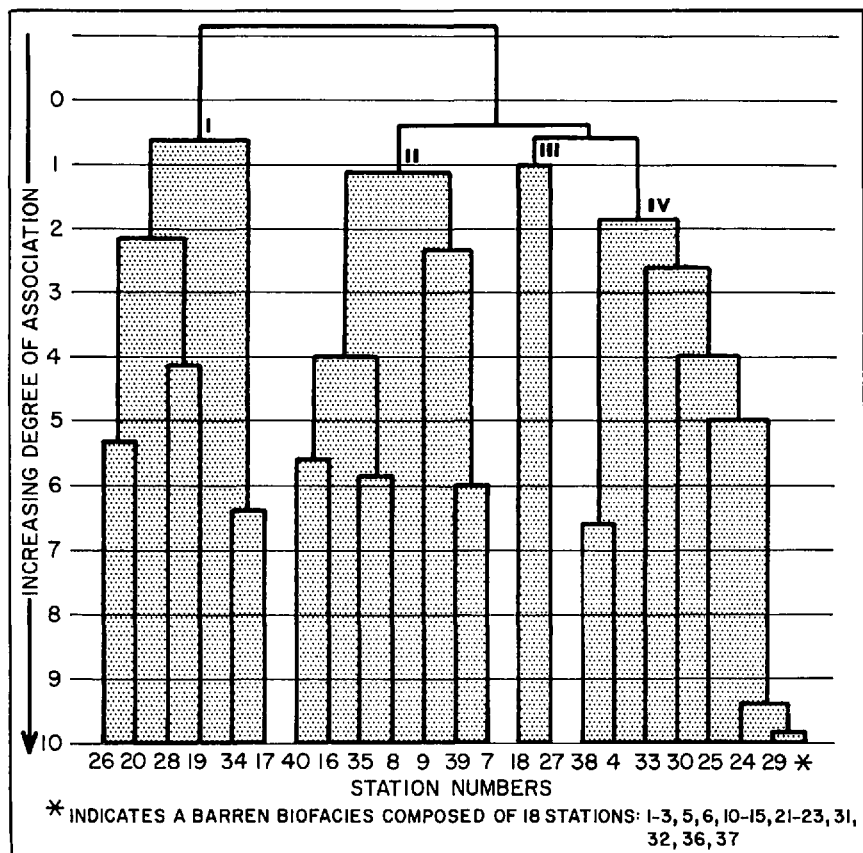


FIGURE 9. Station biofacies clusters (Q-mode).

305-312) was used, coefficients recomputed during each clustering cycle were not based on the previous matrix coefficient values, but rather on values in the initial matrix.

Generally, the value of the coefficient at which variables (species) cluster is considered to be proportional to the degree of association. The clustering level or degree of association between variables can be conveniently represented by a dendrogram. A dendrogram illustrating the results of the R-mode clustering of bryozoan species into "associations" is shown in Figure 8. The degree of association between paired species is indicated along the abscissa. The scale of the abscissa in this study is the value of the correlation coefficient times 10. The ordinate axis of the dendrogram serves only to separate the variables (species). R-mode species clusters having a degree of association greater than 3.5 are indicated

by the shaded portions of the dendrogram in Figure 8. These results and some of the limitations of the clustering technique are discussed below.

Q-mode Cluster Analysis for Biofacies.—Cluster analysis using the Q-mode followed closely the procedure previously outlined for the R-mode analysis. The data matrix was that used for the R-mode analysis, except that it was transposed. Core stations (cases) were treated as variables, and the species (variables) were treated as cases; consequently, core stations were grouped into clusters having similar bryozoan composition.

Sokal & Sneath (1963:142) pointed out that the Q-mode data matrix should be standardized before computation of the correlation coefficients, because the heterogeneous variables (species) are treated as cases and are given equal weight or importance. The data matrix was standardized following the method outlined by Sokal & Sneath. The mean and the standard deviation of each species row were calculated, and each species count was then standardized by dividing its standard deviation into the difference between the species count and the species mean. The standardizing procedure generated a mean of zero and a standard deviation of unity for each species frequency. After standardization of the data matrix, the methods for the computation of correlation coefficients and for the clustering procedure were identical to those used in the R-mode analysis previously described. The dendrogram shown in Figure 9 illustrates the results of the Q-mode clustering. Q-mode station clusters having a degree of association greater than 0.5 are indicated by the shaded portions of the dendrogram in Figure 9.

DISCUSSION OF FAUNAL ANALYSIS

It is necessary to consider some of the inherent limitations of the clustering technique, in order to appraise the meaning of the clusters. Perhaps the most important limitation is the phenomenon of mutual exclusion. The clustering procedure requires that a variable included in one cluster be ineligible for inclusion in any others. In nature, of course, this is not the case with either biofacies or animal associations; usually there is a certain degree of gradation. For example, many species are known to be important biotic elements in more than one association. *Nellia tenella*, the most abundant species in the present study, is found in abundance in all clustered "associations," yet because of the mutual-exclusion phenomenon, it is included in only one "association" cluster.

Another factor which limits the significance of clusters is the reluctance of some variables to enter clusters, either because of their restricted distribution, or their ubiquity. Species which are rare often pair readily, and then tend not to enter into larger clusters. Examples of these limitations are found among both "associations" and biofacies clusters, and are discussed in the following section. These same limitations have been found to be

characteristic also of several previous studies which employed a chi-square test of dependence to establish recurrent groups of bonded species (Fager, 1957, 1963; Cole, 1949; Johnson, 1962; Valentine & Mallory, 1965).

It is apparent from the limitations of cluster analysis that the four species clusters or "associations" defined on the basis of R-mode analysis in this study do not necessarily portray biological associations. To assure that its meaning will not be confused, the term "association," as used here to mean a cluster, is enclosed in quotation marks.

Even when quotation marks are not used, the term association does not necessarily imply biotic or ecological association. In sediments it is seldom possible to determine which species of an assemblage are indigenous and which are present because of postmortem mixing.

Bryozoan Clusters ("Associations").—"Association" I is composed of only two species, *Biflustra savartii* and *Steganoporella magnilabris*. Both species had a spotty distribution in the southern portion of the area, and both were found in minor quantities. These species were found together in moderate quantities at only one station (30), which was in the low-carbonate silt facies. This single occurrence was probably the numerical basis for the clustering of these two species at a rather high (7.1) degree of association. The pair did not cluster with other species until a very low (0.7) association level was reached.

"Association" II is composed of a single species, *Gemelliporella prevailae* n. sp. This species was restricted primarily to shelf-edge sediments in the northern portion of the study area. Because of its unique, restricted distribution, the species remained independent and did not enter a cluster until a low level of association (1.7) was reached.

"Association" III, the largest of the four "associations," is composed of the following species whose combined distribution ranged throughout the calcareous sand facies of the outer shelf:

Cupuladria canariensis

Discoporella umbellata

Scrupocellaria regularis

Metrarabdotos tenue

Nellia tenella

Mamillipora cupula (Discoidal)

Floridina antiqua

Celleporaria sp.

Reteporellina marsupiat

Mamillipora cupula (Conical)

Mamillipora cupula (Encrusting)

Species having discoidal or lunulitiform zoaria characterize this "association." These species include *Cupuladria canariensis*, *Discoporella umbellata* and the discoidal variant of *Mamillipora cupula*.

Other faunal elements of "association" III include the cellariiform species *Nellia tenella* and *Scrupocellaria regularis*. *N. tenella*, the most abundant and widespread species found in this study, is not exclusively restricted to this "association." *Floridina antiqua* occurred in minor

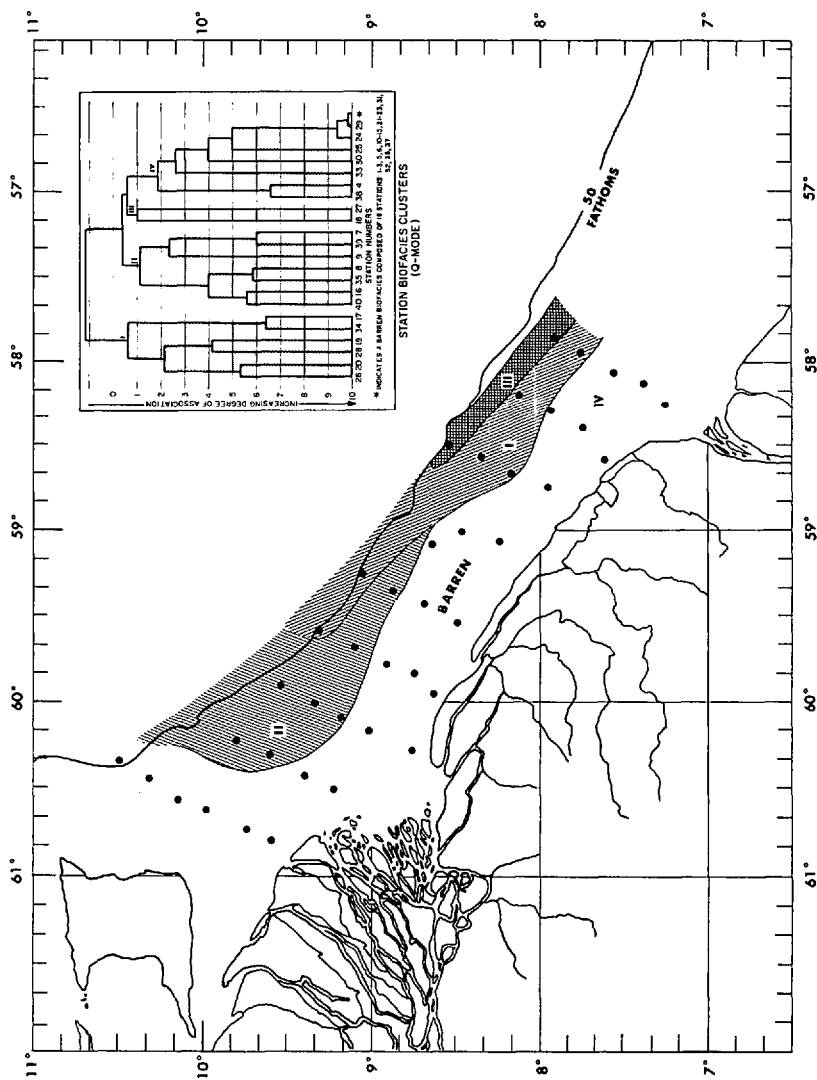


FIGURE 10. Distribution of bryozoan biofacies.

quantities at scattered stations throughout the calcareous sands of the outer shelf, and was often found encrusting a shell-fragment substrate. The distribution of *Celleporaria* sp. and *Metrarabdotos tenue* is directly related to carbonate content of the calcareous sand facies; specimens of these species commonly are stained and worn, and it may be that they have been reworked from shelf-edge biohermal prominences.

The distribution of the conical variant of *Mamillopora cupula* and the eschariform species *Reteporellina marsupiata* is restricted to the calcareous sand facies along the outer shelf east of the Orinoco Delta. The encrusting variant of *M. cupula* was found throughout the calcareous sand facies in moderate quantities on shell fragments and foraminiferal tests; however, it was slightly more abundant east of the Orinoco Delta. It appears that these three associates form a distinct "sub-association" within "association" III that is indigenous to the outer shelf east of the Orinoco Delta.

Canda retiformis, *Gemelliporina glabra*, *Cellaria bassleri*, and *Setosellina goesi* constitute the faunal elements of "association" IV. These associates seem to display a strong preference for carbonate-rich substrates near the shelf-edge biohermal prominences.

Station Clusters (Biofacies).—Four distinct clusters of stations were distinguished by Q-mode cluster analysis (Fig. 9). The distribution of stations belonging to these biofacies conforms in a general manner with sediment facies (Fig. 10).

The distribution of biofacies I and II is similar to the distribution of the calcareous sand facies along the outer shelf. Biofacies I, which includes stations 11, 34, 19, 28, 20, and 26, predominates in the southern portion of the area, while biofacies II, which includes stations 7, 39, 9, 8, 35, 16, and 40, predominates to the north, east of the Orinoco Delta.

Biofacies III includes only two stations, 18 and 27, both of which are located near the shelf edge in the southern part of the study area and are characterized by a high carbonate content. These stations have been interpreted to be located near drowned, Pleistocene bioherms of the shelf edge.

Stations 38, 4, 33, 30, 25, 24, and 29 comprise biofacies IV. This biofacies seems to be a transition into the barren facies characteristic of the silty-clay, and low-carbonate silt environments of the inner shelf, and of the calcareous silty clay facies of the northeastern extreme of the study area.

Relationship Between "Associations" and Biofacies.—In order to assess the significance of the "associations" and the clusters of biofacies, a chi-square test of independence was applied to the observed frequencies of specimens in the four categories of "associations" and the four categories of biofacies. The observed frequency values entered in each cell category were the total number of fragments of all species within a bryozoan

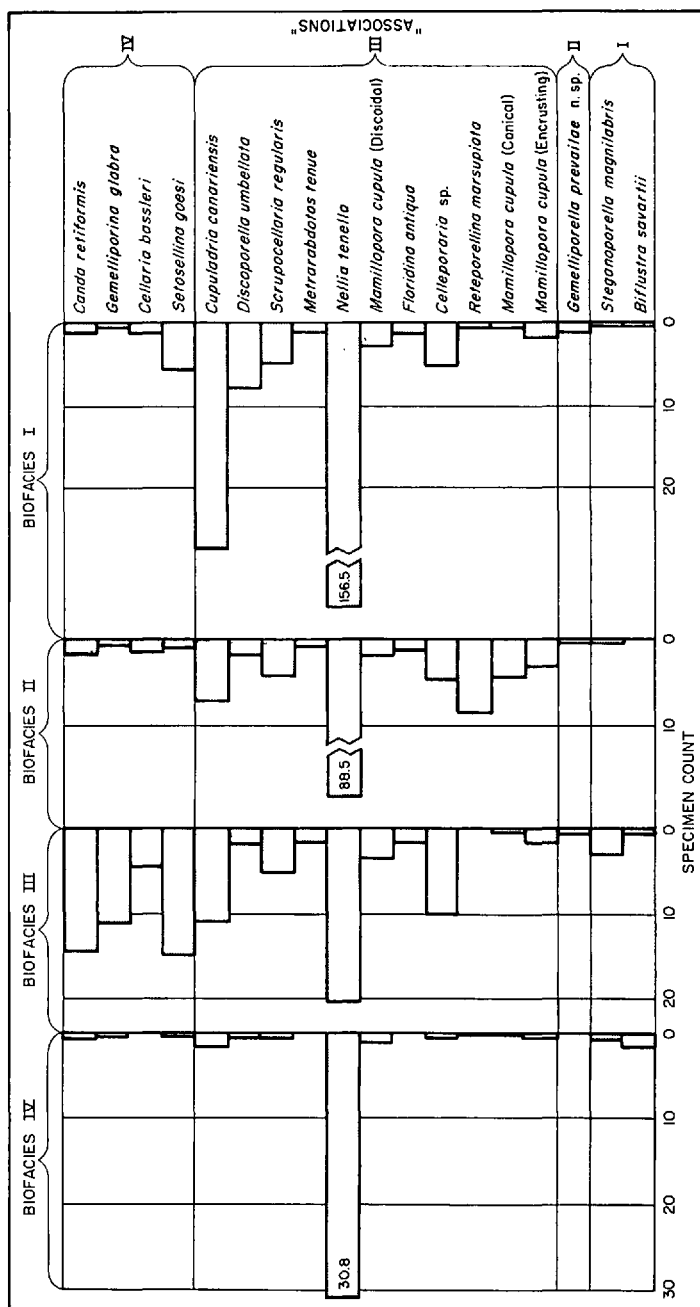


FIGURE 11. Comparison of average species composition of biofacies.

"association" at all core stations included in a given biofacies cluster. The resulting chi-square value of 5,352 at 9 degrees of freedom was ample enough to reject the null hypothesis of independence of categories at the .01 per cent level of significance.

Although the results of the chi-square test indicate a strong general relationship between biofacies and "associations," this does not necessarily mean that there is a biofacies which corresponds to a single "association." An indication of the relationship between the biofacies and bryozoan "associations" clusters is shown graphically in Figure 11, where histograms of the species compositions of the four biofacies are compared. The species composition represented for each biofacies is an average computed from the occurrence of species at the stations which comprise the biofacies.

The characteristic faunal elements of biofacies I and II are the species which are clustered in "association" III. Biofacies I, which occupies the sandy outer shelf along the southern portion of the study area, is characterized by the more abundant and diverse "sub-association" of "association" III. This "sub-association" is characterized by *Cupuladria canariensis* and *Discoporella umbellata*, Bryozoa which have discoidal, lunulitiform zoaria. These species were found in greatest abundance in the southern portion of the calcareous sand facies of the outer shelf. Their abundance gradually diminished in the northern portion of the study area as the calcareous sand graded into the silty clay facies. Species having discoidal zoaria are generally known to be well adapted to sandy substrates (Lagaaij, 1963a; Cook, 1963, 1965a).

Biofacies II occupies the outer shelf east of the Orinoco Delta. It is characterized by fewer lunulitiform specimens, an increase in *Reteporellina marsupiata*, and the abnormal morphological variants of *Mamillopora cupula*. These associates form the less diverse "sub-association" within "association" III. This "sub-association" and its unique faunal elements appear to be related to the sediments of the Holocene deltaic complex of the Orinoco, deposited during lower stands of sea level. During these periods, the Orinoco was depositing deltaic sediments near the shelf edge and along the outer shelf as the sea transgressed. The sediments along the outer shelf east of the Orinoco Delta have greater amounts of fine silts and clays admixed with the sand constituents, and the faunal elements of this biofacies seem adapted to the finer substrate. The conical morphological variant of *M. cupula* is similar to *Fedora nodosa* which is believed (Lagaaij, 1963b) to initiate zoarial growth on a mud-aggregate grain. The encrusting variant was often found on a shell fragment or a large *Amphistigina* test. *Reteporellina marsupiata*, a species having an erect eschariform zoarium, is well suited to finer substrates, provided that at least some sand is present (Harmer, 1934).

Biofacies IV is almost devoid of Bryozoa other than *Nellia tenella*, which reflects a generally poor substrate for bryozoan colonization.

TABLE 2
SUMMARY OF OCEANOGRAPHIC DATA

Consec. sta. No.	Bottom sample No.	BT* slide No.	Position		Surface salinity (‰)	Surface temp. (C)	Bottom temp. (C)	Sonic depth (fathoms)
			Lat. (N)	Long. (W)				
1	1	—	09° 36'	60° 45'	<21.00	29.78	27.57	8.2
2	2	—	09° 45'	60° 41'	<21.00	30.39	24.55	26.8
3	3	—	09° 59'	60° 35'	22.94	30.56	25.78	27.0
4	4	1	10° 09'	60° 31'	33.78	30.06	26.13	33.0
5	5	2	10° 19'	60° 24'	26.92	29.17	23.58	45.0
6	6	3	10° 30'	60° 20'	35.34	29.17	20.82	55.0
7	—	4	10° 40'	60° 14'	35.03	28.33	—	184.4
8	—	5	10° 25'	59° 26'	34.86	28.89	—	697.0
9	—	6	10° 13'	59° 32'	34.85	28.61	—	249.8
10	—	7	10° 05'	59° 37'	34.82	28.89	—	526.1
11	—	8	09° 57'	59° 40'	35.23	28.89	—	379.2
12	—	9	09° 46'	59° 46'	35.24	28.89	—	150.9
13	7	10	09° 33'	59° 52'	34.79	28.61	23.71	50.0
14	8	11	09° 22'	59° 57'	34.36	28.61	25.52	42.0
15	9	12	09° 13'	60° 02'	34.13	29.17	25.60	35.0
16	10	—	09° 02'	60° 08'	<21.00	29.17	24.88	25.0
17	11	—	08° 48'	60° 14'	<21.00	30.61	27.90	7.0
18	12	—	08° 40'	59° 54'	<21.00	31.56	27.42	4.4
19	13	—	08° 46'	59° 47'	34.60	28.67	25.54	15.9
20	14	—	08° 30'	59° 29'	34.74	28.89	27.65	6.0
21	15	—	08° 41'	59° 24'	34.45	29.44	24.34	30.0
22	16	13	08° 53'	59° 18'	35.48	29.44	24.50	41.0
23	17	14	09° 04'	59° 13'	35.29	29.39	24.05	48.0
24	—	15	09° 14'	59° 08'	34.81	29.17	—	242.6
25	—	16	09° 26'	59° 02'	35.27	28.89	—	519.1
26	—	17	09° 37'	58° 56'	35.17	28.61	—	705.8
27	—	18	09° 45'	58° 53'	34.83	28.61	—	788.4
28	—	19	08° 56'	58° 16'	35.26	29.44	—	1120.8
29	—	20	08° 45'	58° 22'	35.34	29.78	—	862.1
30	18	21	08° 33'	58° 27'	35.80	29.72	24.01	50.0
31	19	22	08° 22'	58° 32'	35.87	29.44	24.80	33.0
32	20	—	08° 11'	58° 37'	35.68	30.06	25.72	21.0
33	21	—	07° 58'	58° 44'	35.21	29.44	27.12	7.7
34	22	—	07° 39'	58° 34'	34.51	30.11	27.99	6.0
35	23	—	07° 17'	58° 14'	32.02	29.94	28.25	4.0
36	24	—	07° 24'	58° 07'	35.20	29.61	27.55	11.5
37	25	—	07° 35'	58° 03'	35.97	29.22	28.05	11.0
38	26	—	07° 45'	57° 57'	36.22	28.33	26.26	24.0
39	27	—	07° 56'	57° 51'	35.78	28.67	24.72	30.0
40	—	23	08° 06'	57° 46'	35.66	28.61	—	42.1
41	—	24	08° 17'	57° 40'	35.69	28.67	—	582.0
42	—	25	08° 28'	57° 34'	35.43	28.89	—	942.6
43	—	26	08° 41'	57° 54'	35.36	29.28	—	1107.7
44	—	27	08° 30'	58° 00'	35.85	28.67	—	849.5

* BT = Bathythermograph.

TABLE 2 (CONTINUED)

Consec. sta. No.	Bottom sample No.	BT* slide No.	Position		Surface salinity (‰)	Surface temp. (C)	Bottom temp. (C)	Sonic depth (fathoms)
			Lat. (N)	Long. (W)				
45	—	28	08° 19'	58° 05'	35.72	28.33	—	188.2
46	28	29	08° 08'	58° 11'	35.77	28.72	25.60	25.0
47	29	—	07° 57'	58° 17'	35.57	29.44	26.20	21.0
48	30	—	07° 46'	58° 23'	35.18	29.83	28.23	10.0
49	31	—	08° 15'	59° 02'	34.82	30.22	29.79	6.0
50	32	—	08° 29'	58° 58'	35.50	29.44	29.40	7.0
51	33	30	08° 40'	59° 03'	35.46	29.17	23.99	42.0
52	—	31	08° 50'	58° 48'	35.27	29.28	—	286.7
53	—	32	09° 01'	58° 43'	35.13	29.11	—	810.3
54	—	33	09° 12'	58° 38'	35.11	29.06	—	994.4
55	—	34	10° 15'	59° 05'	34.66	28.89	—	787.3
56	—	35	10° 03'	59° 11'	35.05	29.11	—	767.6
57	—	36	09° 53'	59° 16'	35.00	29.17	—	561.2
58	—	37	09° 41'	59° 21'	35.24	29.17	—	450.7
59	—	38	09° 32'	59° 26'	35.30	29.44	—	250.9
60	34	39	09° 19'	59° 31'	35.33	29.17	23.97	49.8
61	35	40	09° 08'	59° 38'	35.47	29.33	24.94	40.0
62	36	41	08° 58'	59° 44'	34.67	29.28	25.16	35.0
63	37	—	09° 16'	60° 27'	<21.00	30.22	26.86	6.0
64	38	—	09° 26'	60° 23'	<21.00	29.78	24.55	30.0
65	39	—	09° 37'	60° 16'	<21.00	29.83	26.17	35.0
66	40	42	09° 49'	60° 11'	33.94	29.67	24.59	42.0
67	—	43	10° 00'	60° 06'	35.01	29.44	—	125.2
68	—	44	10° 10'	60° 01'	34.96	29.11	—	326.6
69	—	45	10° 21'	59° 54'	34.90	29.17	—	464.3
70	—	46	10° 33'	59° 49'	34.77	29.33	—	585.3

SUMMARY

Four bryozoan "associations" were defined on the basis of R-mode cluster analysis of specimens in samples of surficial sediment from along the Venezuela-British Guiana continental shelf. Of these, only "associations" III and IV appear to be meaningful, while "associations" I and II seem to be numerical misrepresentations due to the aforementioned limitations of the cluster-analysis technique. On the basis of Q-mode cluster analysis, four bryozoan biofacies were defined. The distribution of biofacies I and II is nearly coincident with that of the calcareous sand facies along the outer shelf, and is characterized by the faunal elements of "association" III. Biofacies III is restricted to the two stations (27 and 18) in the proximity of the shelf-edge biohermal prominences, and is characterized by bryozoan "association" IV. No Bryozoa were found in samples from the soft, silty clay facies along the inner shelf. Biofacies IV is transitional between the barren, silty clay facies and the bryozoan-rich sediments of

the outer shelf; it is typified by the species *Nellia tenella*, and by the virtual absence of other bryozoan species.

The calcareous sand facies along the outer shelf provides the substrate for an abundant and diversified bryozoan "association" (III) characterized by an abundance of lunulitiform species, *Cupuladria canariensis*, *Discoporella umbellata*, and *Mamillipora cupula*, but dominated by large quantities of the ubiquitous cellariiform species *Nellia tenella*. Along the outer shelf, east of the Orinoco Delta, the sediments gradually assume a siltier aspect and provide the substrate for a distinctive "sub-association" of Bryozoa. The restricted distribution of the Bryozoa which characterize this "sub-association," *Reteporellina marsupiat*a and the conical morphological variant of *Mamillipora cupula*, suggests that they are adapted to growth on the finer substrate.

A bryozoan "association" (IV), consisting of *Canda retiformis*, *Gemelliporina glabra*, *Cellaria bassleri*, and *Setosellina goesi*, was found in the proximity of the biohermal prominences of the shelf edge. It is not known whether these Bryozoa are relict species which lived during the Pleistocene period of biohermal growth, or whether they have colonized the firm substrate subsequent to the marine transgression and biohermal drowning.

No chitinous parts were found on the bryozoan specimens recorded in this study; however, specimens of most of the species of the outer shelf "association" (III) often retained a fresh, unstained or hyaline appearance. Furthermore, the principal species of the outer-shelf "association" (III) are the same species which characterize the bryozoan fauna found living along the sandy outer shelf between Cape Hatteras and Florida (Dr. F. Maturo, University of Florida, Gainesville, Florida, personal communication). Based on the foregoing observations, it is presumed that most of the bryozoan species of the outer-shelf "association" (III) are elements of a modern living fauna.

Marine geologists are generally agreed that the coarse, sandy facies along the outer shelf seems to be a general and widespread phenomenon, although they may disagree as to its genesis (Kuenen, 1950: 263-267). Inasmuch as the sandy substrate of the outer shelf is widely available for bryozoan colonization, it is interesting to speculate as to the existence of a lunulitiform bryozoan "association," similar to that described herein, widely distributed along the outer continental shelves beneath the warm waters of the oceans.

The strong interrelationships between sediment facies, bryozoan "associations," and biofacies leaves little doubt that, along the Venezuela-British Guiana shelf, the influences of sediment substrate and sedimentation govern the composition of the bryozoan faunules, and overshadow the influence of the hydrographic, ecological parameters of depth and bottom temperature. Bottom water temperature is consonant with depth; however,

the nearly 6°C temperature gradient (29.5°–24.0°C) across the shelf does not seem to be of immediate ecological importance in explaining bryozoan distribution along the shelf. Bottom salinities were not measured, but uniformly normal salinities are presumed to extend throughout the study area, with the only possible exception being the shallow platform of the Orinoco Delta.

Local geological events, such as the retreat of the Orinoco deltaic complex across the shelf, the drowning of the shelf-edge bioherms due to the Holocene transgression, and the existing sedimentary regime, have determined to a large extent the sediment substrates and the distribution of the bryozoan faunules along the Venezuela–British Guiana shelf. The ecological importance of the sediment substrate as a parameter limiting the distribution of marine organisms is well known (Thorson, 1957; Purdy, 1964). Sessile benthonic organisms such as Bryozoa are especially sensitive to sediment substrates (Stach, 1936; Cheetham, 1963; Lagaaij & Gautier, 1965). The findings of this study strongly corroborate the importance of the substrate, and emphasize the serious error that may be committed if the character of the substrate is ignored and temperature or depth gradients are indiscriminately interpreted as being the limiting ecological parameters which explain local faunal distributions.

Order CHEILOSTOMATA Busk

Suborder ANASCA Levinsen

Family Membraniporidae Busk

Genus *Biflustra* d'Orbigny

Biflustra savartii (Audouin)

Fig. 12, a

Flustra savartii Audouin, 1826:240.

Occurrence.—Minor quantities at scattered stations throughout the southern portion of the area.

Remarks.—Nomenclature follows Lagaaij (1952) who found, upon re-examination of type material, that the well-known genus *Acanthodesia* Canu & Bassler is a junior synonym of *Biflustra*.

Family Antroporidae Vigneaux

Genus *Antropora* Norman

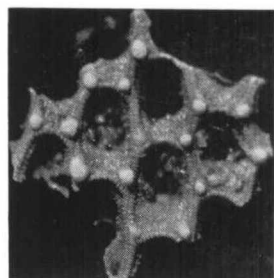
Antropora typica (Canu & Bassler)

Fig. 12, b

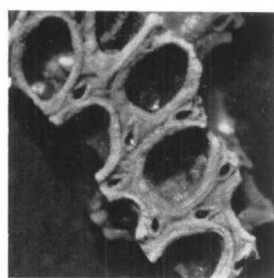
Dacryonella typica Canu & Bassler, 1928:57, pl. 5, figs. 4-8; pl. 32, figs. 11, 12.

Occurrence.—Very minor quantities along the shelf edge and outer shelf in the southern portion of the area.

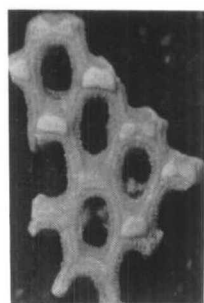
Remarks.—No ovicelled specimens were observed.



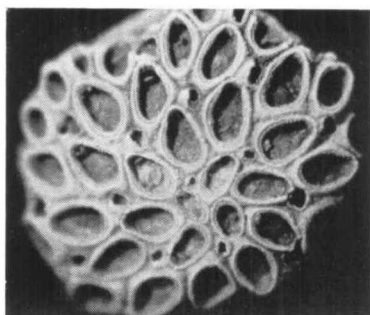
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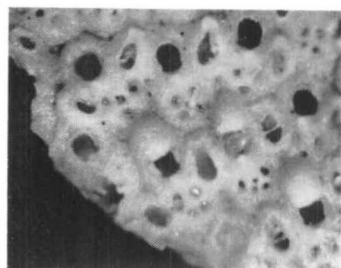
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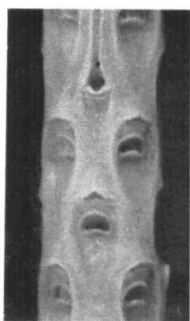
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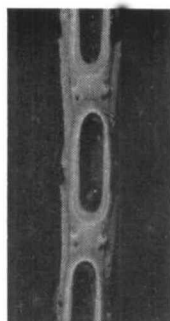
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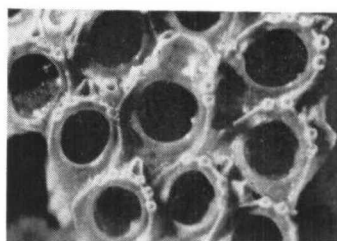
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K

Family Calloporidae Norman

Genus *Crassimarginatella* Canu*Crassimarginatella leucocypha* Marcus

Fig. 12, c

Crassimarginatella leucocypha Marcus, 1937:46, pl. 8, fig. 20a; pl. 9, figs. 20b, 20c.*Occurrence*.—Very minor quantities scattered along the outer shelf.*Remarks*.—Specimens consist of small fragments with sediment-filled zooecia.Genus *Parellisina* Osburn*Parellisina curvirostris* (Hincks)

Fig. 12, k

Membranipora curvirostris Hincks, 1862:29, pl. 7, fig. 4.*Occurrence*.—Two fragmentary specimens from along the outer shelf in the northern portion of the area.*Remarks*.—Hyperstomial ovicells are present on nearly every zooecium. No interzooecial avicularia are recorded from the scant available material.Genus *Retevirgula* Brown*Retevirgula tubulata* (Hastings)

Fig. 12, j

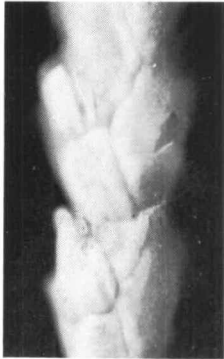
Pyrulella tubulata Hastings, 1930:709, pl. 6, figs. 20-26.*Occurrence*.—One small, fragmentary specimen from the low carbonate silt facies of the inner shelf in the southern portion of the area.*Remarks*.—The specimen compares favorably with Lagaij's (1963b) figured specimen from the Gulf of Mexico (USNM 648014).

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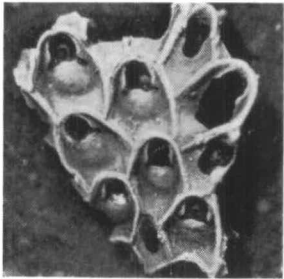
FIGURE 12. a, *Biflustra savartii* (Audouin): zoarial fragment with four complete zooecia; LSU 8085; $\times 23$. b, *Antropora typica* (Canu & Bassler): zoarial fragment showing zooecia and interzooecial avicularia; LSU 8086; $\times 23$. c, *Crassimarginatella leucocypha* Marcus: zoarial fragment showing four complete zooecia; LSU 8087; $\times 23$. d, *Setosellina goesi* (Silen): zoarium encrusting foraminiferan test; LSU 8088; $\times 11$. e, *Tremogasterina lanceolata* Canu & Bassler: zoarial fragment showing several zooecia, three ovicelled, and several having large elongate avicularia; LSU 8089; $\times 11$. f, *Cellaria bassleri* Hastings: internode fragment showing parts of seven zooecia; at least four are ovicelled, and one vicarious avicularium; LSU 8090; $\times 31$. g, *Nellia tenella* (Lamarck): quadrate internode fragment showing frontal view of portions of three zooecia, and two pairs of proximolateral avicularia; LSU 8091; $\times 31$. h, *Canda retiformis* Pourtales: branched zoarial fragment showing five complete zooecia; LSU 8092; $\times 31$. i, *Chaperia condylata* Canu & Bassler: several zooecia showing both proximal pedunculate and medial distal triangular avicularia, one ovicelled zooecium; LSU 8093; $\times 23$. j, *Retevirgula tubulata* (Hastings): zoarial fragment of a single zooecium showing dorsal tubular processes; LSU 8094; $\times 40$. k, *Parellisina curvirostris* (Hincks): zoarial fragment showing two complete zooecia, both ovicelled; LSU 8095; $\times 23$.



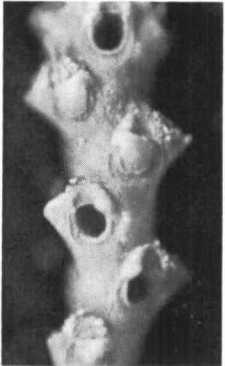
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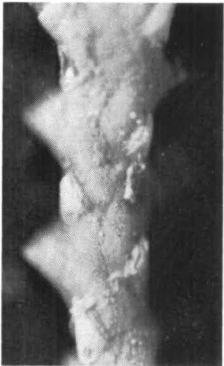
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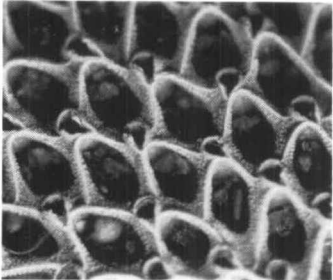
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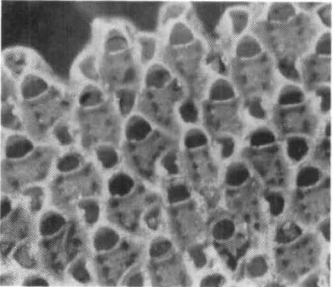
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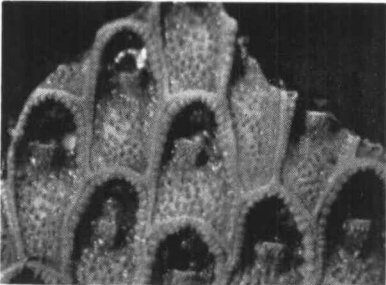
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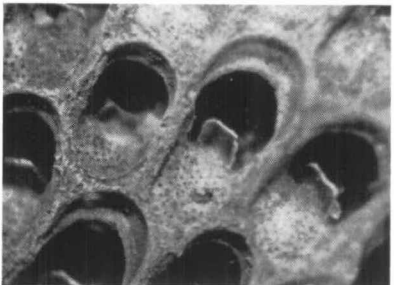
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Family Selenariidae Busk

Genus *Setosellina* Calvet*Setosellina goesi* (Silén)

Fig. 12, d

Heliodoma goesi Silén, 1942:2, pl. 1, figs. 3, 4.

Occurrence.—Moderate abundance in the outer-shelf calcareous sand facies throughout the southern portion of the area.

Remarks.—This species usually encrusts a coarse quartz grain, or calcareous shell fragment, or *Amphistegina* test.

Family Chaperiidae Jullien

Genus *Chaperia* Jullien*Chaperia condylata* Canu & Bassler

Fig. 12, i

Chaperia condylata Canu & Bassler, 1930:44, pl. 9, figs. 1-3.

Occurrence.—Minor quantities along the shelf edge in the southern portion of the area.

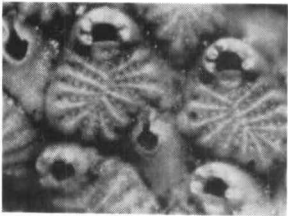
Remarks.—Ovicelled zooecia bear one or two avicularia. Pedunculate avicularia are displayed on the proximal gymnocyst of several zooecia. The presence of these avicularia serves to distinguish *C. condylata* from *C. patula* (Hincks) which was reported from the Gulf of Mexico by Lagaaij (1963:176-177, pl. 2, fig. 2). The basal portions of the four to six hollow oral spines are often obliterated by abrasion of the mural rim. The only other reported occurrence of this species outside the eastern Pacific was by Cheetham & Sandberg (1964) from Quaternary sediments of the Gulf of Mexico.

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FIGURE 13.—a-b, *Scrupocellaria regularis* Osburn: a, frontal aspect of internode fragment; LSU 8096; $\times 46$. b, reverse side of same fragment showing two large vibracula; $\times 46$.—c, *Floridina antiqua* (Smitt): zoarial fragment having seven autozooecia and three avicularia; LSU 8098, $\times 23$.—d-e, *Scrupocellaria maderensis* Busk: d, frontal side of internode fragment showing three zooecia having scutum; LSU 8097; $\times 46$. e, reverse side of same fragment showing several small vibracula; $\times 46$.—f, *Cupuladria canariensis* (Busk), sensu lato; enlarged frontal view of zoarium showing arrangement of zooecia and distal vibracula; LSU 8099; $\times 23$.—g, *Discoporella umbellata* (Defrance): frontal side of zoarium showing arrangement of zooecia and distal vibracula; LSU 8100; $\times 23$.—h, *Labioporella granulosa* (Canu & Bassler): zoarial fragment showing portions of ten zooecia; LSU 8101; $\times 23$.—i, *Steganoporella magnilabris* (Busk): zoarial fragment showing three complete zooecia, two A-zooecia, one B-zooecium; LSU 8102; $\times 23$.



A



B



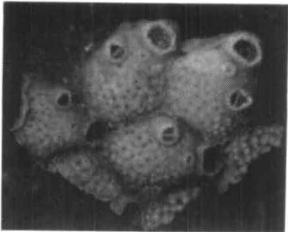
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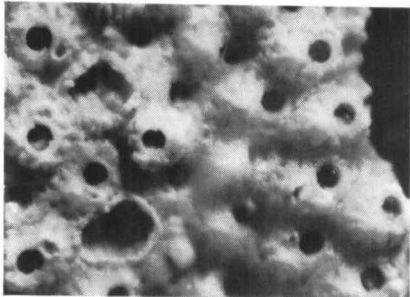
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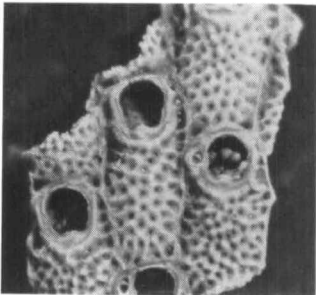
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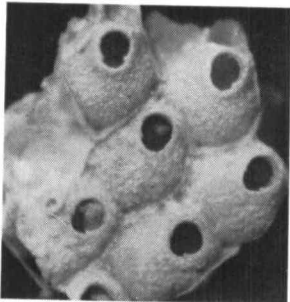
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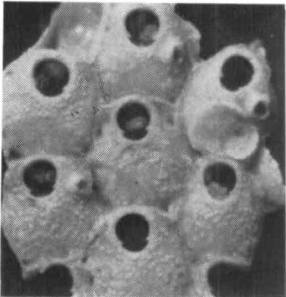
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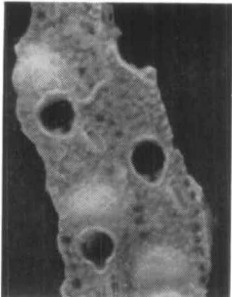
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Family Onychocellidae Jullien

Genus *Floridina* Jullien*Floridina antiqua* (Smitt)

Fig. 13, c

Mollia antiqua Smitt, 1873:12, pl. 2, fig. 73.

Occurrence.—Spotty distribution throughout the carbonate sand facies along the outer shelf, where it occurs in moderate abundance.

Genus *Smittipora* Jullien*Smittipora levinseni* (Canu & Bassler)

Fig. 14, c

Velumella levinseni Canu & Bassler, 1917:26.

Occurrence.—One small, fragmentary specimen from the calcareous silty clay facies along the northern outer shelf.

Family Hiantoporidae MacGillivray

Genus *Tremogasterina* Canu*Tremogasterina lanceolata* Canu & Bassler

Fig. 12, e

Tremogasterina lanceolata Canu & Bassler, 1928:48, pl. 13, fig. 9.

Occurrence.—Minor quantities, scattered, from the calcareous sand facies of the outer shelf.

Family Cupuladriidae Lagaaij

Genus *Cupuladria* Canu & Bassler*Cupuladria canariensis* (Busk), sensu lato

Fig. 13, f

Cupuladria canariensis Busk, 1859:66, pl. 23, figs. 6-9.

←

FIGURE 14.—a-b, *Criblilaria* aff. *C. radiata* (Moll): a, zoarial fragment showing six zooecia and three interzooecial avicularia; LSU 8103; $\times 23$. b, enlargement of same specimen; $\times 40$.—c, *Smittipora levinseni* (Canu & Bassler): a small zoarial fragment showing one zooecium and avicularium; LSU 8104; $\times 23$.—d-e, *Gemelliporina glabra* (Smitt): d, showing erect cylindrical zoarial form; LSU 8105; $\times 11$. e, enlargement of same zoarial fragment showing details of several zooecia; $\times 23$.—f, *Microporella ciliata* (Pallas), sensu lato: four zooecia, each showing a single frontal avicularium and median ascopore; LSU 8106; $\times 31$.—g, *Hippoporidra janthina* (Smitt): zoarial fragment showing several zooecia; LSU 8107; $\times 31$.—h, *Hippopetraliella marginata* (Canu & Bassler): three zooecia showing lateral oral avicularia; LSU 8108; $\times 23$.—i-j, *Gemelliporella prevailae* n. sp.: i, zoarial fragment with six zooecia, one showing lateral avicularium; paratype, LSU 8109; $\times 31$. j, zoarial fragment with seven zooecia, three showing lateral avicularium and one having broken ovicell; holotype, LSU 8110; $\times 31$.—k, *Remulostoma? signatum* (Waters): three zooecia, two having ovicells, all with frontal avicularia; LSU 8111; $\times 31$.

Occurrence.—Very abundant throughout the calcareous sand facies of the outer shelf.

Remarks.—Specimens of several different forms, such as discussed by Cheetham & Sandberg (1964:1021), are for convenience considered as one species, *C. canariensis*, following Lagaaij (1963a). Worn and stained specimens are often found together with white, fresh-appearing specimens.

Genus *Discoporella* d'Orbigny
Discoporella umbellata (Defrance)
Fig. 13, g

Lunulites umbellata Defrance, 1823:361, pl. 47, figs 1, 1a, b.

Occurrence.—Abundant throughout the calcareous sand facies along the outer shelf; most abundant in the southern portion of the area.

Family Steganoporellidae Hincks
Genus *Steganoporella* Smitt
Steganoporella magnilabris (Busk)
Fig. 13, i

Membranipora magnilabris Busk, 1852:vi (explanation of Pl. 65) pl. 65, fig. 4.

Occurrence.—Minor quantities scattered throughout the outer-shelf, calcareous sand facies and the low-carbonate silt facies in the southern portion of the area.

Remarks.—The opercula and mandibles are important diagnostic features for species of *Steganoporella*. Chitinous parts are not present in the material studied. According to Cook (1964), the insertion of the cryptocyst into the basal wall of the zooecium distinguishes this species from *S. buskii* Harmer which is characterized by the insertion of the cryptocyst into the distal wall.

Genus *Labioporella* Harmer
Labioporella granulosa (Canu & Bassler)
Fig. 13, h

Siphonoporella granulosa Canu & Bassler, 1928:69, pl. S, fig. 1.

Occurrence.—Minor quantities along the outer shelf in the southern portion of the area.

Family Cellariidae Hincks
Genus *Cellaria* Ellis & Solander
Cellaria bassleri Hastings
Fig. 12, f

Cellaria bassleri Hastings, 1947:232 (dated April 1946, but published January 1947).

Occurrence.—Modest quantities in calcareous sand facies along the outer shelf; most abundant in carbonate-rich sediment near the shelf edge.

Family Farciminariidae Busk

Genus *Nellia* Busk*Nellia tenella* (Lamarck)

Fig. 12, g

Cellaria tenella Lamarck, 1816:135.

Occurrence.—Abundant throughout the calcareous sand facies of the outer shelf, and in minor quantities in the low-carbonate silt facies of the southern portion of the area.

Remarks.—This species is widely distributed throughout modern tropical and warm-temperate seas. Many workers, apparently unsure of the character of Lamarck's species, have applied the junior synonym, *N. oculata* (Busk), to this species. It is the most widespread, and numerically-abundant species along the shelf. It was found throughout the area, except in cores from the barren, silty clay facies of the inner shelf, and core 18 at the shelf edge.

Family Scrupocellariidae Levinsen

Genus *Scrupocellaria* van Beneden*Scrupocellaria maderensis* Busk

Fig. 13, d, e

Scrupocellaria maderensis Busk, 1860:280.

Occurrence.—Minor quantities in the outer-shelf calcareous sand facies in the southern portion of the area.

Remarks.—No ovicelled specimens were found.

Scrupocellaria regularis Osburn

Fig. 13, a, b

Scrupocellaria regularis Osburn, 1940:384.

Occurrence.—Moderate quantities throughout the calcareous sands of the outer shelf; slightly greater abundance near the shelf edge.

Remarks.—Most specimens were stained and filled with sediment.

Genus *Canda* Lamouroux*Canda retiformis* Pourtales

Fig. 12, h

Canda retiformis Pourtales, 1867:110.

Occurrence.—Modest quantities throughout the calcareous sand facies in the southern portion of the area.

Remarks.—Worn and stained specimens occur along with hyaline, fresh-appearing specimens.

Suborder ACANTHOSTEGA Levinsen

Family Cribrilinidae Hincks

Genus *Cribrilaria* Canu & Bassler*Cribrilaria* sp., aff. *C. radiata* (Moll)

Fig. 14, a, b

?Eschara radiata Moll, 1803:63, pl. 4, figs 17a-i.

Material.—Figured specimen, LSU 8103.

Diagnosis.—*Cribrilaria* having cribrate kenozoecia without orifice, and interzoecial avicularia with strong condyles, broad gymnocystal front, and large, spatulate rostrum directed distally and truncated at the end.

Description.—Zoarium encrusting. Zooecia ovate; frontal shield inflated, composed of six to eight pairs of distinct, thick costae separated by small, evenly-spaced lacunae; median lacuna, just proximal to orifice, appears ascoporelike. Orifice semicircular, with five to seven distal spines. Interzoecial avicularia with broad gymnocystal front and well-developed condyles; rostrum spatulate, directed distally, and terminally truncate. Kenozoecia approximately one-fourth the size of autozoecia, with cribrate frontal shield, lacking orifice. Ovicelled specimens not present.

Measurements.—Figured specimen, LSU 8103.

	Number measured	Mean (mm)	Observed range (mm)
Zooecial length (Lz)	8	0.40	0.36-0.43
Zooecial width (Iz)	8	0.33	0.30-0.36
Oral length (ho)	7	0.04	0.03-0.04
Oral width (lo)	7	0.07	0.06-0.07
Avicularian length (Lav)	6	0.26	0.17-0.36
Kenozoecia length (LK)	2	0.17	0.15-0.19
Kenozoecia width (lk)	2	0.13	0.10-0.16

Occurrence.—Trace quantities in carbonate-rich sediments at the shelf edge.

Discussion.—The introduction of a new species does not appear appropriate at this time because of the scant material available for examination. No ovicelled zooecia were found.

Suborder *ASCOPHORA* Levinsen

Family Petraliellidae Harmer

Genus *Hippopetraliella* Stach

Hippopetraliella marginata (Canu & Bassler)

Fig. 14, h

Petraliella marginata Canu & Bassler, 1928:80, pl. 16, figs. 6-11.

Occurrence.—Very minor quantities in calcareous sand facies along the outer shelf.

Family Hippoporinidae Bassler

Genus *Gemelliporina* Bassler

Gemelliporina glabra (Smitt)

Fig. 14, d, e

Gemellipora glabra Smitt, 1873:37-40, pl. 11, figs. 208-210.

Occurrence.—Moderate abundance, especially in carbonate-rich sediments from the shelf edge in the southern portion of the area.

Family Schizoporellidae Jullien
Genus "*Stylopoma*" Levinsen
"*Stylopoma spongites*" Levinsen
Fig. 15, d

Eschara spongites Pallas, 1766:45 (part).

Occurrence.—Minor quantities scattered along the outer shelf.

Remarks.—This species is well known and widespread throughout warm waters of both the Atlantic and Pacific. The nomenclatural confusion associated with this taxon is outlined in considerable detail by Cheetham & Sandberg (1964). Their nomenclatural assignment has been retained in this report.

Genus *Escharina* Milne Edwards
Escharina pesanseris (Smitt)
Fig. 15, a

Hippothoa pes anseris Smitt, 1873:43, pl. 7, figs. 159-160.

Occurrence.—Very minor quantities in the vicinity of the shelf-edge calcareous sand facies.

Family Cleidochasmatidae Cheetham & Sandberg
Genus *Cleidochasma* Harmer
Cleidochasma porcellanum (Busk)
Fig. 16, d

Lepralia porcellana Busk, 1860:283, pl. 31, fig. 3.

Occurrence.—Three fragmentary specimens in carbonate-rich sediments of the shelf edge.

Genus *Hippoporidra* Canu & Bassler
Hippoporidra janthina (Smitt)
Fig. 14, g

Lepralia edax forma *janthina* Smitt, 1873:64, pl. 2, figs 224, 225.

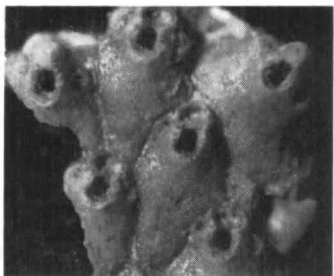
Occurrence.—Minor quantities in scattered samples along the outer shelf.

Remarks.—This species closely resembles *H. edax* (Busk), but Cook (1964) distinguished it by a wider, shallower proximal sinus and more numerous frontal pores. Material has a stained and abraded appearance.

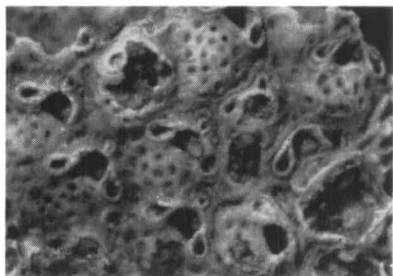
Genus *Gemelliporella* Canu & Bassler
Gemelliporella prevailae n. sp.
Fig. 14, i, j

Material.—Holotype LSU 8110; paratype LSU 8109.

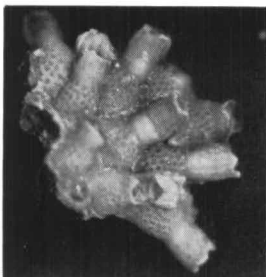
Diagnosis.—*Gemelliporella* having a finely granular frontal wall and sub-circular orifice, with shallow, semicircular sinus set off by small, proximally inclined condyles. The short, distally-directed avicularian rostrum distinguishes this species from *G. inflata* Osburn.



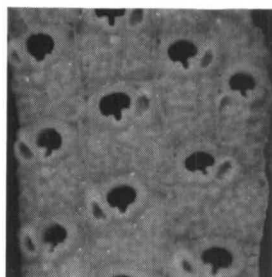
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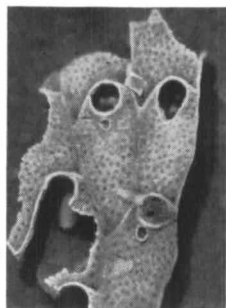
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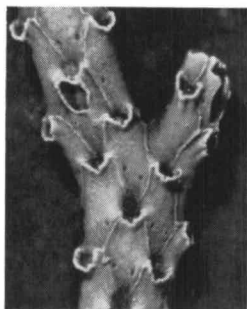
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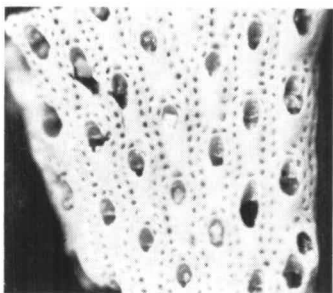
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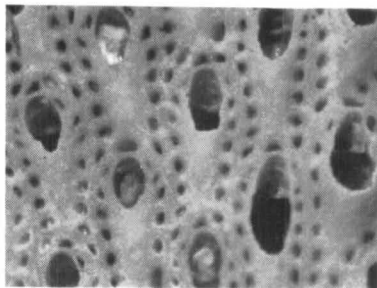
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Description.—Zoarium encrusting. Zooecia hexagonal, slightly inflated, and separated by deep grooves. Frontal wall thin, minutely granular with a row of small, indistinct areolar pores around the margin. Orifice sub-circular with small, proximally inclined condyles which define a shallow, semicircular sinus occupying the proximal one-third of the orifice; peristome subdued and without spines. Adventitious avicularia low, pedunculate, lateral, single, commonly along the proximolateral border of the orifice; rostrum short, directed distally. Hyperstomial ovicell prominent, globular, and minutely perforate.

Measurements.—Holotype LSU 8110; paratype LSU 8109.

	Number measured	Mean (mm)	Observed range (mm)
Zooecial length (Lz)	12	0.42	0.38-0.46
Zooecial width (Iz)	13	0.39	0.36-0.45
Oral length (ho)	13	0.15	0.15-0.16
Oral width (lo)	13	0.13	0.12-0.15
Avicularian length (Lav)	4	0.08	0.06-0.10

Occurrence.—Edge of shelf (30-45 fathoms).

Discussion.—Canu & Bassler (1919) introduced *Gemelliporella punctata* as the type-species by monotypy without a generic diagnosis. Subsequently, Lagaaij (1963b) restudied the species and presented a generic diagnosis. The author, however, has for convenience followed the generic concept of Osburn (1952).

This species is named after the USS PREVAIL, the Oceanographic survey vessel from which the material for this study was collected.

Family Microporellidae Hincks

Genus *Microporella* Hincks

Microporella ciliata (Pallas), sensu lato

Fig. 14, f

Eschara ciliata var. B Pallas, 1766:38.

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FIGURE 15. a, *Escharina pesanseris* (Smitt): zoarial fragment showing parts of six zooecia, all ovicelled; LSU 8112; $\times 23$. b, *Anarthropora coccinella* (Canu & Bassler): zoarial fragment showing ten zooecia, all having paired lateral avicularia and a small distal oral avicularium; LSU 8113; $\times 31$. c, *Lagenicella marginata* (Canu & Bassler): zoarial fragment showing several zooecia; LSU 8114; $\times 23$. d, "*Stylopoma spongites*" Levinsen: zoarial fragment showing several zooecia, all having lateral avicularia; LSU 8115; $\times 31$. e, *Tremoschizodina lata* (Smitt): three zooecia; LSU 8116; $\times 23$.—f-g, *Reteporellina marsupiala* (Smitt): f, frontal aspect of erect branching zoarium having several zooecia, all showing paired frontal pores; LSU 8117; $\times 23$. g, reverse dorsal side of same zoarium; $\times 23$.—h, *Tubucellaria* sp.: internode fragment showing several zooecia; LSU 8118; $\times 11$.—i-j, *Metrarabdotos tenue* (Busk): i, zoarial fragment showing several zooecia; LSU 8119; $\times 11$. j, enlargement of same specimen, $\times 31$.

Occurrence.—Very minor quantities from shelf edge.

Remarks.—*M. ciliata* is distinguished from the closely related species *M. pontifica* Osburn by the peristome on the ovicelled zooecia; it encloses both orifice and ascopore in *M. pontifica*, but only the orifice of *M. ciliata* (Osburn, 1952). Unfortunately, no ovicelled zooecia were found in the present material. In the absence of distinguishing criteria, this material is tentatively assigned to *M. ciliata*.

Family Smittinidae Levinsen
Genus *Parasmittina* Osburn
Parasmittina spathulata (Smitt)
Fig. 16, a

Escharella jacotini var. *spathulata* Smitt, 1873:59, pl. 10, figs. 199, 200.

Occurrence.—Minor quantities from carbonate-rich sediments near the shelf edge.

Genus *Rimulostoma* Vigneaux
Rimulostoma? signatum (Waters)
Fig. 14, k

Smittia signata Waters, 1889:17, pl. 3, figs 4-6.

Occurrence.—Very minor quantities scattered throughout the calcareous sand facies of the outer shelf.

Remarks.—The generic assignment follows Cheetham & Sandberg (1964).

Family Phylactellidae Jullien
Genus *Lagenicella* Cheetham & Sandberg
Lagenicella marginata (Canu & Bassler)
Fig. 15, c

Lagenipora marginata Canu & Bassler, 1930: 36, pl. 6, figs. 2, 3.

Occurrence.—Two small, fragmentary specimens from carbonate-rich sediments of the shelf edge.

Family Tubucellariidae Busk
Genus *Tubucellaria* d'Orbigny
Tubucellaria sp.
Fig. 15, h

Occurrence.—Two fragments from carbonate-rich sediments of the shelf edge.

Remarks.—The two fragmentary specimens do not exhibit diagnostically specific characters.

Family Reteporidae Smitt
Genus *Reteporellina* Harmer

Reteporellina marsupiata (Smitt)

Fig. 15, f, g

Retepora marsupiata Smitt, 1873:67, pl. 13, figs. 211-212.

Occurrence.—Moderate abundance in the calcareous sand facies of the outer shelf in the northern portion of the area.

Family Adeonidae Hincks

Genus *Metrarabdotos* Canu*Metrarabdotos tenue* (Busk)

Fig. 15, i, j

Smittia tenuis Busk, 1884:150, pl. 20, fig. 1.

Occurrence.—Moderate abundance in calcareous sand facies along the shelf edge and outer shelf.

Genus *Anarthropora* Smitt*Anarthropora coccinella* (Canu & Bassler)

Fig. 15, b

Adeonellopsis coccinella Canu & Bassler, 1923:161, pl. 24, figs. 5-8.

Occurrence.—Two small fragmentary specimens along the outer shelf in the southern portion of the area.

Remarks.—This species, not reported heretofore from sediments younger than Miocene, is similar to *A. stellata* (Smitt), a recent Florida species.

Family Cheiloporinidae Bassler

Genus *Tremoschizodina* Duvergier*Tremoschizodina lata* (Smitt)

Fig. 15, e

Gemellipora lata Smitt, 1873:36.

Occurrence.—Two small fragmentary specimens in the northern portion of the area.

Genus *Hippaliosina* Canu*Hippaliosina rostrigera* (Smitt)

Fig. 16, e

Escharella rostrigera Smitt, 1873:57, pl. 10, figs. 203-205.

Occurrence.—Only one small fragment in the calcareous sand facies in the southern portion of the area.

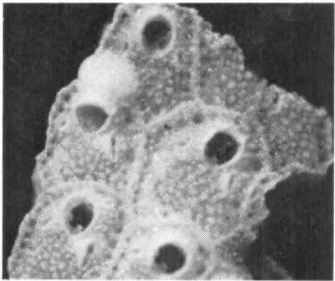
Family Mamilloporidae Canu & Lecointre

Genus *Mamillopora* Smitt*Mamillopora cupula* Smitt

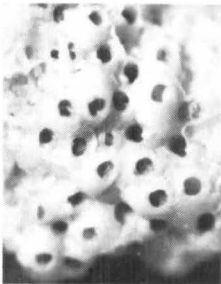
Fig. 16, f, g, h, i

Mamillopora cupula Smitt, 1873:33, pl. 7, figs. 146, 147.

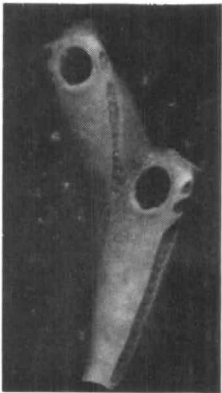
Occurrence.—Abundant and widely distributed in the calcareous sand facies of the outer shelf.



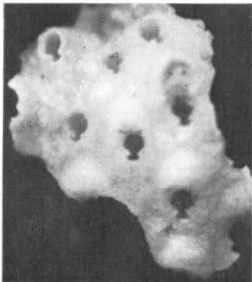
A



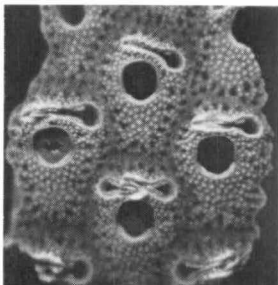
B



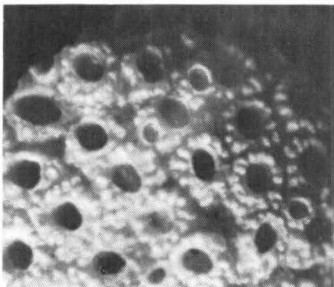
C



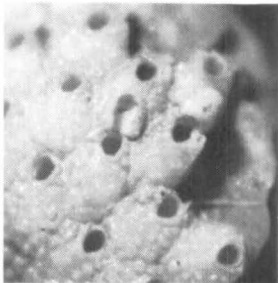
D



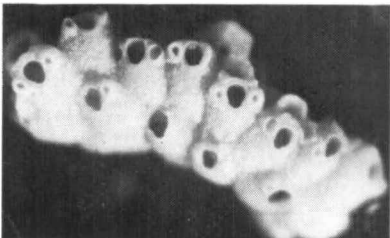
E



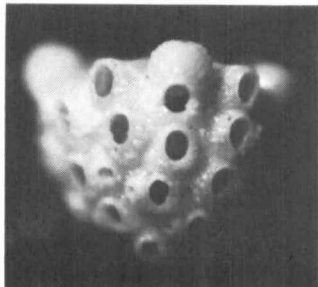
F



G



H



I

Remarks.—Three morphological variants of this species were observed. They differ in zoarial form, and are often found to coexist in the same sample. The discoidal zoarial variant is considered the “normal” form, and has the zoarial configuration most often illustrated by previous authors. The conical variant is distinctly different in shape and has a large, exposed, axial cavity. This variant superficially resembles *Fedora nodosa* Silen (described by Lagaaij, 1963b) but differs in that the “special chambers” which persistently occur on *F. nodosa* are not present, and hyperstomial ovicells, lacking in *F. nodosa*, are present. The encrusting variant is the most abundant and widespread form of this species. It usually encrusts a shell fragment or a test of *Amphistegina*. The colony grows radially from a central ancestrular pit. The encrusting variant also differs from other forms in that the hyperstomial ovicell is not deeply embedded in the distal zooecium. The zooecia are elongate and have a more fully developed tuberculate frontal wall, while in the normal, discoidal variant the frontal wall is reduced to little more than a broad, tuberculate peristome. It may be speculated that the morphological variant which the species assumes is related to the size or type of substrate upon which the larvae settle; the conical growth form may be assumed where growth is initiated on a mud-aggregate grain (Lagaaij, 1963b); the encrusting form may be assumed when the larvae settle on excessively large grains or shell fragments. The substrate for the normal form is a very small particle which is usually not externally visible.

Family Celleporariidae Harmer

Genus *Celleporaria* Lamouroux

Celleporaria sp.

Fig. 16, b

Occurrence.—Abundant along the outer shelf; greatest abundance in carbonate-rich sediments near the shelf edge.

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FIGURE 16. a, *Parasmittina spathulata* (Smitt): zoarial fragment showing five zooecia, one ovicelled; LSU 8120; $\times 31$. b, *Celleporaria* sp.: several zooecia shown on zoarial fragment; LSU 8121; $\times 11$. c, *Vittaticella uberrima* Harmer: frontal view showing two zooecia, both having vittae and avicularia; LSU 8122; $\times 46$. d, *Cleidochasma porcellanum* (Busk): seven complete zooecia shown, three ovicelled; LSU 8123; $\times 31$. e, *Hippaliosina rostrigera* (Smitt): four complete zooecia, three having single avicularium, one having paired avicularia; LSU 8124; $\times 31$. f, *Mamillopora cupula* Smitt: frontal view of a fragment of a “normal” discoid morphological variant showing several zooecia and frontal avicularia; LSU 8125; $\times 31$. g, *Mamillopora cupula* Smitt: frontal view of “encrusting” variant, two zooecia ovicelled; LSU 8126; $\times 31$. h, *Mamillopora cupula* Smitt: frontal view of “encrusting” variant showing lateral avicularia, several zooecia with broken ovicells; LSU 8127; $\times 31$. i, *Mamillopora cupula* Smitt: frontal view of “conical” variant, distal zooecia having large plainly visible ovicells, showing several lateral avicularia; LSU 8128; $\times 31$.

Remarks.—The specimens are usually stained and worn, and, due to abrasion, the diagnostic peristomial features are lost and specific assignment is not possible.

Family Vittaticellidae Harmer

Genus *Vittaticella* Maplestone

Vittaticella uberrima Harmer

Fig. 16, c

Vittaticella uberrima Harmer, 1957:772, pl. 50, figs. 4, 5, 15.

Occurrence.—Very minor quantities scattered in calcareous sand facies of the outer shelf.

Remarks.—The specimens consist of biglobulus internodes. No ovicelled specimens were observed.

SUMARIO

ANÁLISIS PALEOECOLÓGICO DE BRIOZOOS CHEILOSTOMATOS DE LOS SEDIMENTOS PROCEDENTES DE LA PLATAFORMA DE VENEZUELA—GUAYANA INGLESA

La plataforma continental de Venezuela—Guayana Inglesa es una amplia llanura que desciende ligeramente hacia el mar con sedimentos de superficie caracterizados por facies de arcilla fangosa cerca de la costa, que en dirección al mar se convierten gradualmente en arena calcárea. En la porción meridional del área de estudio, líneas y prominencias de carbonatos biohermales se presentan en el borde de la plataforma. Estos son considerados relictos biohermales del Pleistoceno de una posición más baja del mar.

Los briozoos cheilostomatos encontrados en muestras de sedimentos procedentes de 40 estaciones a lo largo de la plataforma, han sido descritos y su presencia ha sido investigada numéricamente. Se emplearon técnicas de agrupamiento modo-Q para establecer biofacies basándose en estaciones que tienen faunas similares y métodos de agrupamiento modo-R para establecer “asociaciones” agrupando especies que se presentan conjuntamente. Se discuten biofacies y “asociaciones” de Bryozoa y su distribución y composición y se comparan con varios parámetros ambientales. Dos “asociaciones” de significación y cuatro biofacies han resultado de la técnica de agrupamiento.

Se notó una fuerte interrelación entre asociaciones de briozoos, biofacies y sustrato de sedimentos. La facie de arcilla fangosa a lo largo de la plataforma interior está virtualmente libre de briozoos.

Entre las arcillas fangosas estériles y la arena calcárea rica en briozoos de la plataforma exterior, hay una biofacie transicional que esencialmente está libre de briozoos que no sean *Nellia tenella*.

Se encuentra a lo largo de la plataforma una asociación de briozoos caracterizada por especies que tienen zoaria lunuliforme, principalmente *Cupuladria canariensis*, *Discoporella umbellata* y *Mamillipora cupula*. Una "sub-asociación" en el substrato algo más fino a lo largo de la plataforma exterior al este del Delta del Orinoco ha sido identificada y está caracterizada por *Reteporellina marsupiata* y la variante cónica de *M. cupula*.

En estaciones cerca del borde de la plataforma en la vecindad de las prominencias biohermales ha sido reportada una "asociación" de *Candaretiformis*, *Gemelliporina glabra*, *Cellaria bassleri* y *Setosellina goesi*. La diversidad de especies alcanza un máximo en la proximidad de los biohermos. Los biohermos pueden proveer una fuente para la redistribución y revisión de la contribución de la fauna a la "asociación" característica de la plataforma exterior.

Se concluye que el substrato de sedimento es el principal factor que influencia la distribución de briozoos a lo largo de la plataforma. No se puede discernir el efecto de los parámetros hidrográficos ambientales de temperatura y profundidad calculados a base de la distribución de la fauna. De estar presente, el mismo se halla completamente enmascarado por la influencia del substrato sedimentoso.

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